Morphology, taxonomy, and nomenclature of the *Chrysomyxa ledi* complex and related rust fungi on spruce and Ericaceae in North America and Europe[1]

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Abstract: Rust fungi in the genus *Chrysomyxa* Unger occur in boreal forests of the northern hemisphere on Pinaceae (mostly *Picea* A. Dietr.), and most species alternate to angiosperm hosts in the Ericaceae. About 30 species are known worldwide. Although several species are economically important pathogens of spruce and rhododendrons, knowledge about species delineations, relationships among species on different continents, and life cycles is lacking. A group of species with similar spore size, including the *Chrysomyxa ledi* de Bary complex, was re-examined using field observations, inoculation experiments, and light and scanning electron microscopy. In addition to host specificity, characters found useful in species delineation were urediniospore and aeciospore size and shape, and ornamentation of spores and the aecial peridium. Detailed descriptions are given for eight *Chrysomyxa* species, including synonyms, types, distribution, relationship to other species, and disease impact. The members of the *C. ledi* complex are considered separate species: *Chrysomyxa ledi* on *Ledum palustre*, ***Chrysomyxa nagodhii*** sp.nov. on *Ledum groenlandicum* and *Ledum decumbens*, ***Chrysomyxa neoglandulosi*** sp.nov. on *Ledum glandulosum*, *Chrysomyxa cassandrae* on *Chamaedaphne calyculata*, *Chrysomyxa rhododendri* on *Rhododendron* spp., and ***Chrysomyxa vaccinii*** comb.nov. on *Vaccinium parvifolium*. *Chrysomyxa chiogenis*, with similar spore size, is included for comparison. A previously unrecognized small-spored species, ***Chrysomyxa reticulata*** sp.nov., is described on *Ledum* spp. and *Rhododendron* spp. Evidence is presented that *C. reticulata* spreads from native *Ledum* spp. in North America to cultivated rhododendrons. A new anamorphic species, ***Peridermium zilleri***, likely belonging in *Chrysomyxa*, is described on *Picea sitchensis* from coastal British Columbia.

Key words: Uredinales, *Rhododendron*, needle rust, *Ledum*, systematics.

Résumé : Les champignons de la rouille du genre *Chrysomyxa* Unger sont fréquents sur les Pinaceae (surtout *Picea* A. Dietr.) des forêts boréales de l'hémisphère nord, et la plupart des espèces ont des hôtes alternatifs angiospermes appartenant aux Ericaceae. On en reconnaît environ 30 espèces au monde. Bien que plusieurs espèces soient des organismes pathogènes économiquement importants sur les épicéas et les rhododendrons, les connaissances sur la définition des espèces, sur les relations entre espèces sur différents continents et sur les cycles vitaux font défaut. En utilisant des observations aux champs, des inoculations expérimentales ainsi que la microscopie photonique et par balayage au laser, les auteurs ont réexaminé un groupe d'espèces ayant des spores de dimension semblable, incluant le complexe *Chrysomyxa ledi* de Bary. En plus de la spécificité de l'hôte, on note que la dimension et la forme des aeciospores et des urédospores, ainsi que l'ornementation sporale et le péridium des aecidies, sont des caractères utiles pour définir les espèces. L'auteur présente des descriptions détaillées pour huit espèces de *Chrysomyxa* incluant les synonymes, les types, les distributions, les relations avec les autres espèces et l'impact des maladies. On considère comme espèces distinctes celles du complexe *C. ledi* : *C. ledi* sur *Ledum palustre*, ***Chrysomyxa nagodhii*** sp.nov. sur *Ledum groenlandicum* et *Ledum decumbens*, ***Chrysomyxa neoglandulosi*** sp.nov. sur *Ledum glandulosum*, *Chrysomyxa cassandrae* sur *Chamaedaphne calyculata*, *Chrysomyxa rhododendri* sur *Rhododendron* spp., et ***Chrysomyxa vaccinii*** comb.nov. sur *Vaccinium parvifolium*. Pour fin de comparaison, on inclut le *Chrysomyxa chiogenis*, portant des spores de même dimension. L'auteur décrit une espèce non reconnue précédemment et ayant de petites spores, le ***Chrysomyxa reticulata*** sp.nov. sur *Ledum* spp., qu'on retrouve sur les rhododendrons cultivés, en Amérique du Nord. L'auteur décrit

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finalement une nouvelle espèce anamorphe, le ***Peridermium zilleri***, appartenant vraisemblablement au genre *Chrysomyxa*, et venant sur le *Picea sitchensis* des régions côtières de la Colombie canadienne.

Mots clés : Urédinales, *Rhododendron*, rouille des aiguilles, *Ledum*, systématique.

[Traduit par Rédaction]

Introduction

Rust fungi (Uredinales) in the genus *Chrysomyxa* Unger cause needle and cone diseases on conifers, mostly *Picea* A. Dietr. Two species have been described also on hemlock (*Tsuga*) and one on *Keteleeria*, a subtropical conifer with 11 species in China. All conifer hosts belong to subfamily Abietoideae of the family Pinaceae (LePage 1993). Of the approximately 30 species in the genus, most are heteroecious, alternating to plants in the Ericaceae s.l. (including Rhododendroideae, Empetraceae, Vaccinioideae, and Pyroloideae). Many of these plants have evergreen leaves in which the rusts overwinter as mycelium. Some species have a circumboreal distribution, whereas others have a more limited distribution in subalpine or boreal forest regions of a single continent. Depending on the species, location, and duration of infection, these rusts can cause severe defoliation, brooming, seed destruction, or reduced tree height and diameter and may contribute to tree death. These fungi can be particularly damaging when spruce species are introduced into nonindigenous parts of the world (Takahashi and Saho 1985) or under intensive cultivation of host plants (Sutherland 1990, 1991; Singh and Carew 1990). Several *Chrysomyxa* species produce their uredinia and (or) telia on cultivated rhododendrons and cause economically important diseases on these hosts (Gould et al. 1955; Gould 1966; Bennell 1985).

The telia of *Chrysomyxa* are produced in early spring and germinate without a period of dormancy to produce basidiospores, which infect the conifer host. The telial sori are gelatinous or waxy, pulvinate or tongue-like structures that erupt through the host epidermis. Teliospores are one celled, smooth walled, and borne in chains. Uredinia of most or all species are surrounded by an inconspicuous peridium consisting of one or more layers of thin-walled pseudoparenchymatous cells (Berndt 1999). The urediniospores and aeciospores are produced by basipetal succession to form chains of spores alternating with intercalary cells. With few exceptions, aeciospores and urediniospores in a given species have similar ornamentation, typically annulate warts, and this character can be used to infer relationship where the connection between spore states has not been proven experimentally. The aecia are peridermioid. Spermogonia are subepidermal and usually determinate and flask shaped.

Identification of *Chrysomyxa* to the species level is often difficult for several reasons. The telia provide few characters for distinguishing among species. Different heteroecious species may have similar urediniospore and aeciospore size, and they may occur on the same spruce species as well as the same telial hosts. Confusion also occurs because of the superficial resemblance of needle-infecting *Pucciniastrum* spp. to *Chrysomyxa* spp. However, several characters can be used to distinguish the aecia and spermogonia of the two genera. In *Pucciniastrum* needle rusts the spermogonia are pale, almost colorless, and subcuticular (seen in needle cross sections) (Hiratsuka and Cummins 1963), whereas in *Chrysomyxa* spp. the spermogonia tend to become a darkly pigmented brown or reddish brown as they age, and they arise subepidermally. *Pucciniastrum* needle infections appear earlier in the spring (June in western Canada) and aeciospores are pale yellow, whereas chrysomyxa rusts produce aecia later (July to August or even later in some species) and the aeciospores are salmon colored to deep reddish orange, depending on the species.

Savile (1950, 1955) described the North American species of *Chrysomyxa*, but no well-illustrated, up-to-date account exists. Although the biology of certain species occurring in Europe is fairly well-known, their relationship to species occurring elsewhere has not been elucidated adequately. Historically, the hypophyllous rusts on *Ledum* spp. in North America have been considered conspecific with the Eurasian *Chrysomyxa ledi* de Bary (Arthur and Kern 1906; Sydow and Sydow 1912–1915; Arthur 1934; Boyce 1943). Savile (1950, 1955) created varieties of *C. ledi* to accommodate the North American rusts on *Ledum* spp. This was based on similar spore size and difficulty in distinguishing the aecial states on spruce needles. *Chrysomyxa cassandrae*, *Chrysomyxa vaccinii*, and *Chrysomyxa rhododendri* were also described as varieties of *C. ledi* for the same reasons. However, because the variety names for the North American *Ledum* rusts were not validly published, the name *C. ledi* is still used for some of these taxa. These names have been applied inconsistently, and there is confusion in the identity of these fungi. With the increasing movement of host plants, both *Picea* and ericaceous hosts, to new locations, clear species definitions are important to disease diagnosis and control.

A major objective of this study is to provide detailed, illustrated descriptions of the above *Chrysomyxa* species and others with similar spore size, and keys to their identification. On the basis of host and morphological differences, I consider the members of the *C. ledi* complex (Savile 1950, 1955) to be separate species: *C. ledi*, *C. rhododendri* (de Bary 1879), and *C. cassandrae* (Tranzschel 1893) as originally defined; *C. ledi* var. *vaccinii* Savile as *C. vaccinii* comb.nov.; and the North American hypophyllous *Ledum* rusts as *Chrysomyxa neoglandulosi* sp.nov. (on *L. glandulosum*) and *Chrysomyxa nagodhii* sp.nov. (on *Ledum groenlandicum* and *Ledum decumbens*). Additional new species are *Chrysomyxa reticulata* sp.nov., previously unrecognized on *Ledum* spp. and cultivated rhododendrons in North America, and a new *Peridermium*, *Peridermium zilleri* anam.nov., on *Picea sitchensis* (Bong.) Carrière. The latter most likely belongs to *Chrysomyxa*.

Characters useful in taxonomy of *Chrysomyxa*

Aeciospores and urediniospores

Spore ornamentation is considered taxonomically useful at

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both the genus and species level in rust fungi (e.g., Hiratsuka and Kaneko 1975; Sato and Sato 1982; Lee and Kakishima 1999), and this was confirmed for the genus *Chrysomyxa*. Features of spore surface morphology found to be fairly consistent within species are shape and size of warts; the presence and characteristics of leg-like or web-like appendages at the base of, and often connecting, the warts; number of annuli on warts; and presence and characteristics of a longitudinal groove or flat area, or a raised cap covering the warts over part of the spore. Several of these characters, mainly elucidated by scanning electron microscopy (SEM), but often also visible by light microscopy (LM), have seldom been included in descriptions for *Chrysomyxa* species. Additional characters that are useful, but may be quite variable under certain circumstances, are spore size and shape, wall thickness, and wart height. The distance between warts, a character used by Savile (1950, 1955), is very difficult to measure accurately by LM, and can vary greatly in a given spore, especially within or adjacent to the above-mentioned grooves, or when warts are joined laterally. The position and number of germ pores, considered useful taxonomic characters at the species level in many rust fungi (Kaneko and Hiratsuka 1982), are not easily observed in *Chrysomyxa*.

Sorus morphology and aecial peridium

For several species, gross morphology of the aecia may be a useful character, including size and whether sori are confluent. The ornamentation of inner and outer peridial surfaces, in addition to that of the aeciospores, is useful taxonomically.

Teliospores and basidiospores

Although teliospore size may be characterisitic for each species, it is difficult to measure accurately because spores lengthen as they mature, and once they germinate to produce basidia and basidiospores, they collapse. Size and shape of basidiospores are fairly consistent within a species, but reports of size are affected by whether the apiculus was included.

Spermogonia

In *Chrysomyxa* on spruce needles, spermogonia form along the stomatal lines and they are always subepidermal; they are usually determinate and more or less globose or triangular in cross section, i.e., with a concave or flat hymenium (group I, type 1 or 2; Hiratsuka and Cummins 1963). The width and height of the spermogonia, although somewhat variable, in conjunction with characters of the aecia and aeciospores, may aid in identification.

Materials and methods

Field observations were made of most spore states of *C. cassandrae*, *C. ledi*, *C. nagodhii*, *C. neoglandulosi*, and *C. reticulata*. Fresh telia were available for *C. cassandrae*, *C. nagodhii*, *C. neoglandulosi*, and *C. reticulata*, and therefore spruce needles were artificially inoculated in a greenhouse or outdoors in Edmonton, Alberta, to obtain spermogonia and aecia connected with a particular ericaceous host. Natural infection by needle rusts has not been observed within several kilometers of the location of these experiments. Disease-free spruce (*Picea glauca* (Moench) Voss, *Picea mariana* (Mill.) BSP, *Picea pungens* Engelm., and (or) *Picea engelmannii* Parry ex Engelm.) grown from seed or transplanted from field locations were inoculated. Host leaves bearing telia were stored in a refrigerator at 4°C on moist filter paper in Petri dishes. For inoculation, these leaves were placed, telia side down, directly onto needles of newly opened spruce buds, or several leaves or shoots were suspended above the tree on a wire cage so that basidiospores would be shed onto young needles. Trees were misted with distilled water, covered with a plastic bag for 48–72 h, then uncovered. They were observed for several weeks for disease development. For each experiment, several additional, uninoculated, trees were kept in the same location to serve as controls. In some cases, young spruce that were growing within 1 m of infected ericaceous hosts in the field were potted and kept in a greenhouse for observation of development of natural infections. When authentic material on spruce was not available locally, material inoculated by earlier workers was obtained from various herbaria.

Herbarium specimens were examined from the following institutions: Northern Forestry Centre, Edmonton, Alberta (CFB, WINF(M), CAFB), and Pacific Forestry Centre, Victoria, British Columbia (DAVFP), Canadian Forest Service; the Arthur Herbarium, Purdue University, Lafayette, Indiana (PUR); U.S. National Fungus Collection, Beltsville, Maryland (BPI); National Mycological Herbarium, Eastern Cereal and Oilseed Centre, Agriculture and Agri-food Canada, Ottawa (DAOM); the Royal Botanic Gardens, Kew, U.K. (K); the Vascular Plant Herbarium, Department of Biological Sciences, University of Alberta, Edmonton, Alberta (ALTA); and the Finnish Forestry Research Institute, Rovaniemi, Finland. Only specimens for which slide mounts were made are listed in the Appendix; in most cases, many more were examined for gross morphology with a dissecting microscope.

For LM, spores and hand sections of infected plant material were mounted in lactophenol or lactophenol – cotton blue. Spore measurements (15–20 mature spores per sample) were made at 400× using brightfield or phase-contrast microscopy; spermatia, wart height, and wall thickness were measured under oil at 1000×. When fresh material was available, basidiospores were collected by suspending leaves with telia above a microscope slide in a moist chamber. The basidiospores were measured without the apiculus. Measurements that were beyond the typical range are given in parentheses in the species descriptions. For measurements of aeciospores and urediniospores, the mean and standard deviation are provided. Spore color of fresh material was compared with Kornerup and Wanscher (1978) and is given as a color name and number.

For SEM, aeciospores or urediniospores were dusted onto aluminum stubs covered with adhesive tabs attached (Electron Microscopy Sciences), coated with gold, and examined with an Hitachi S-510 SEM operated at 15 or 25 kV. SEM images were captured using Quartz PCI software, version 4.0. Light microscope images were made by digitizing black and white photographic negatives made from Kodak TMAX 100 or 400 film, or by digitizing 35-mm color slides and converting them to black and white. Adobe Photoshop 5.0 was used to adjust image contrast and to compose all plates.

Keys to the species

The eight species of *Chrysomyxa* described herein, and *Peridermium zilleri*, all produce localized needle infections on *Picea* and leaf-spot diseases on various angiosperm hosts, and they all have mean aeciospore and urediniospore lengths of <30 µm. Keys to aid in their identification are given below.

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Key to the telial and uredinial states

1*a*. Telia and (or) uredinia on *Ledum* or *Rhododendron* . . . 2
1*b*. Telia and (or) uredinia on *Chamaedaphne*, *Gaultheria*, or *Vaccinium* . . . 6

2*a*. Urediniospores with almost smooth surface . . . *C. nagodhii*
2*b*. Urediniospores with separate warts over most of surface . . . 3

3*a*. Urediniospores mostly globose or subglobose with very fine, even warts on surface; no groove, cap, or smooth area . . . *C. neoglandulosi*
3*b*. Urediniospores with a longitudinal groove, cap, or smooth area . . . 4

4*a*. Urediniospores mostly <20 µm long, with a reticulate area on part of spore . . . *C. reticulata*
4*b*. Urediniospores mostly 18–30 µm long . . . 5

5*a*. Urediniospores with a narrow longitudinal groove and tapered warts elsewhere . . . *C. ledi*
5*b*. Urediniospores with a poorly defined longitudinal smoother area and cylindrical warts elsewhere . . . *C. rhododendri*

6*a*. Uredinia and (or) telia on *Vaccinium* or *Gaultheria* (Vaccinioideae) . . . 7
6*b*. Uredinia and (or) telia on *Chamaedaphne* . . . *C. cassandrae*

7*a*. Urediniospores tend to be elongated, ellipsoidal, ovoid, or oblong, (16–)20–32 × 11–20 µm ($\bar{x}$ = 25 × 16 µm), on *Vaccinium* . . . *C. vaccinii*
7*b*. Urediniospores tend to be globose, occasionally elongated, 15–32 × 13–21 µm ($\bar{x}$ = 22 × 16 µm), on *Gaultheria*. *C. chiogenis*

Key to the aecial and spermogonial states on *Picea*

1*a*. Spermogonia lacking . . . 2
1*b*. Spermogonia present . . . 3

2*a*. Aeciospores fusiform, 23–39(–44) × 10–19 µm ($\bar{x}$ = 30 × 14 µm), with broad longitudinal smooth area . *Peridermium zilleri*
2*b*. Aeciospores ellipsoidal or ovoid, (15–)20–28 × 13–18 µm ($\bar{x}$ = 23 × 15 µm), smooth at ends . . . *C. chiogenis*

3*a*. Aeciospores mostly <20 µm long, with smoother longitudinal cap over one side of spore . . . *C. reticulata*
3*b*. Aeciospores mostly >20 µm long . . . 4

4*a*. Aeciospores mostly globose rather than elongated; warts very narrow and tapering, almost echinulate; no groove or smooth area . . . *C. neoglandulosi*
4*b*. Aeciospores variously shaped, with annulate warts; with a groove, cap, or smooth area over part of spore . . . 5

5*a*. Aeciospores 20–38 × 15–28 µm ($\bar{x}$ = 28 × 22 µm), with a narrow longitudinal groove . . . *C. ledi*
5*b*. Aeciospores mostly <27 µm long ($\bar{x}$ = 23–24 × 18–19 µm), with annulate warts and a longitudinal or indistinct smoother area over part of spore . . . 6

6*a*. Aeciospores with a poorly defined longitudinal smoother stripe . . . *C. rhododendri*
6*b*. Aeciospores with a well-defined longitudinal cap along one side . . . 7

7*a*. Longitudinal cap slightly rough, with a smooth edge . . . *C. nagodhii*
7*b*. Longitudinal cap with broad shallow warts and a broken edge . . . *C. cassandrae*

Species descriptions[4]

Chrysomyxa cassandrae Tranzschel, Trav. Soc. Nat. St. Petersburg (=Trudi St. Petersb. Obshch. Estestvoisp., Otd. Bot.), Sect. Bot. 23: 28. 1893. Figs. 1A–1H

=*Uredo cassandrae* Peck & Clinton, in Peck, Ann. Rep. N.Y. State Mus. 30: 54. 1878. [Based on uredinia; specimen bears telia (Savile 1950)]

≡*Chrysomyxa ledi* de Bary var. *cassandrae* (Peck & Clinton) Savile, Can. J. Res. C, 28: 324. 1950.

≡*Melampsoropsis cassandrae* (Peck & Clinton) Arthur, N. Am. Flora, 7: 119. 1907. [telia described]

=*Caeoma cassandrae* Gobi, Scr. Bot. Horti Univ. Petropol. I: 166–180. 1886. [*fide* Tranzschel 1893]

=*Caeoma cassandrae* Rostr., Medd. Bot. For. Kjøbenhavn, 2: 90. 1888. [Based on uredinia]

=*Peridermium consimile* Arthur & Kern, Bull. Torrey Bot. Club, 33: 427. 1906.

TYPE: On *Chamaedaphne calyculata* (L.) Moench., Levashovo, near St. Petersburg, Russia, 24 May 1892, W. Tranzschel (not seen). The whereabouts of this collection could not be determined. Savile (1955) designated one of Peck's specimens of *Uredo cassandrae* as the neotype, based on the presence of telia: on *Chamaedaphne calyculata* (as *Cassandra calyculata* (L.) D. Don), Center, New York, June 1871, Clinton (NYS).

HOSTS AND DISTRIBUTION: *Chamaedaphne calyculata* is the only telial host of this rust. Reports of *C. cassandrae* on *Andromeda* spp. (*Pieris* spp.) (Arthur 1907; Sydow and Sydow 1912; Anonymous 1960) are questionable (Jackson 1918; Farr et al. 1989). They appear to have originated with Arthur (1907), but were later corrected (Arthur 1925). *Pucciniastrum myrtilli* Arthur (*Uredo andromedae* Cooke),

[4] Abbreviations and symbols used: D.B.O.S., D.B.O. Savile; nom.nud., nomen nudum, an invalid name; P.E.C., P.E. Crane; p.p., pro parte, in part; Q.C.I., Queen Charlotte Islands; s.l., sensu lato, in the broad sense; s.s., sensu stricto, in the strict sense; W.G.Z., W.G. Ziller; Y.H., Y. Hiratsuka; ! indicates a type collection was seen by the author.

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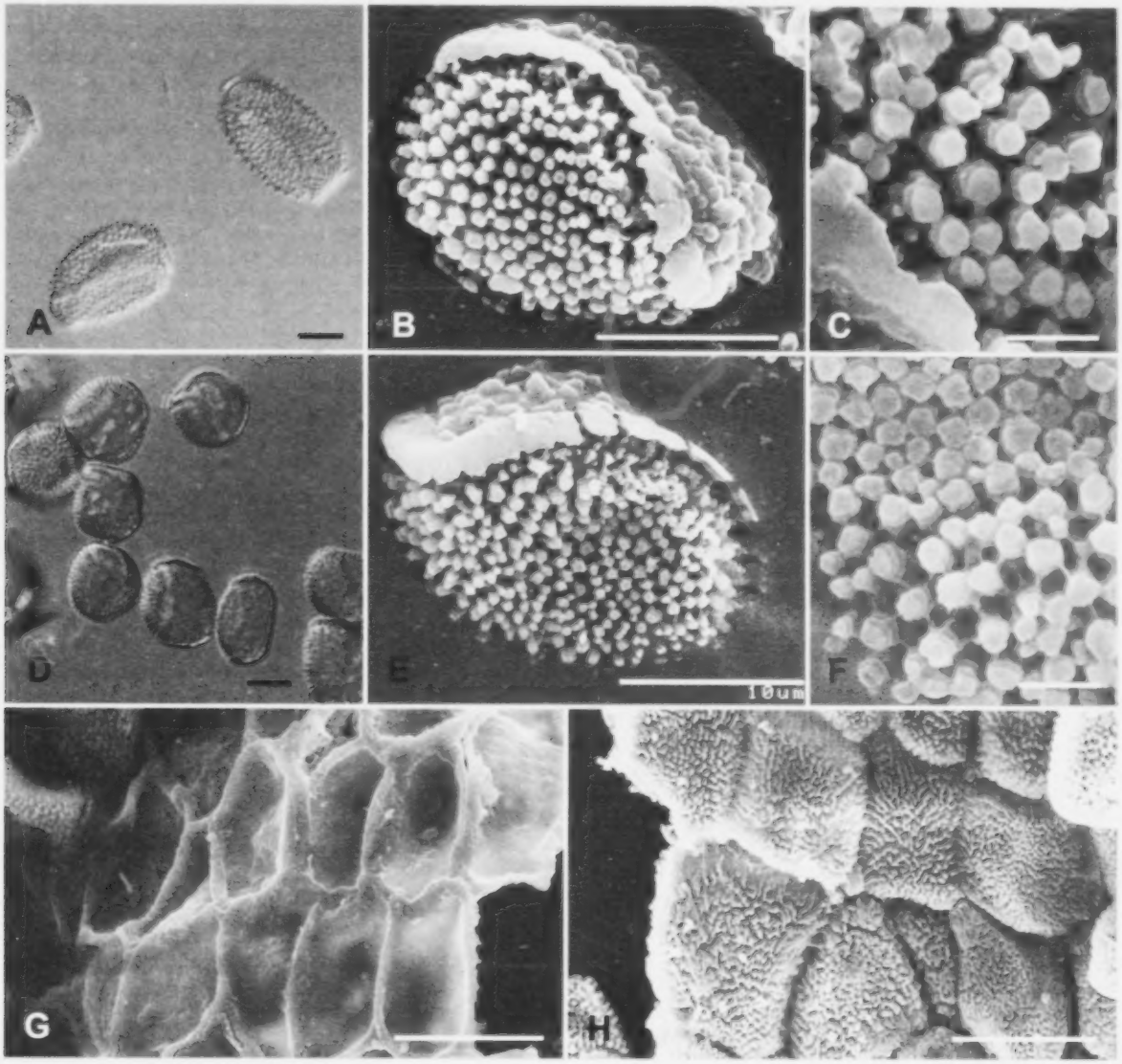
Fig. 1. *Chrysomyxa cassandrae*. (A–C) Urediniospores: (A) by LM; (B) single spore (SEM), showing broad longitudinal smoother area or cap; (C) cylindrical warts. (D–F) Aeciospores: (D) by LM; (E) single spore (SEM), showing cap with bumps and broken edge; (F) crowded, cylindrical warts with smooth or rough tops. (G, H) Aecial peridium: smooth outer surface (G) and densely ornamented inner surface (H). In Figs. 1A, 1B, 1D, and 1E, scale bar = 10 μm; in Figs. 1C and 1F, scale bar = 2 μm; in Figs. 1G and 1H, scale bar = 20 μm.



which has echinulate urediniospores (Jackson 1918), was likely misidentified as a chrysomyxa. *Chrysomyxa cassandrae* occurs throughout the North Temperate Zone wherever *Chamaedaphne calyculata* occurs, independent of host alternation. This includes northern Canada (all provinces and territories), and the U.S.A. (Alaska, and eastern states south to Pennsylvania), northern Europe (Denmark, Sweden, Finland, Lithuania, Russia (Karelia, Kamchatka, Sakhalin)), and Japan. It has not been reported on spruce in Japan (Hiratsuka et al. 1992). Aecial hosts are *Picea abies* (L.) Karst., *P. mariana*, *P. pungens*, and *P. glauca*. This study extends the known range of this rust on spruce to western Canada. In addition to field collections on both hosts in central Alberta, telia and (or) uredinia were found on *Chamaedaphne calyculata* in vascular plant collections (CAFB and ALTA) from northern Alberta, Saskatchewan, and Manitoba. Therefore, it is probably much more common on spruce than previously thought, but it could be mistaken for *C. nagodhii*. It could also be overlooked on *Chamaedaphne calyculata*, which is a small inconspicuous shrub that occurs much more sporadically than *L. groenlandicum*; it is characteristic of black spruce peatlands and flooded wetlands (Beckingham and Archibald 1996).

Description

On *Chamaedaphne*. Uredinia and telia hypophyllous on leaves of previous year, uredinia occasionally on petiole or main leaf vein, causing brown leaf spot. Uredinia in groups, discrete,

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separate from or forming in telia, circular, 0.25–0.75 mm in diam., subepidermal, or when on petiole, arising beneath several layers of collenchyma cells; having an inconspicuous peridium of collapsed, thin-walled cells. Urediniospores ellipsoidal, ovoid, lenticular, or occasionally subglobose, with a broad cap at one or both ends, part of a broad flat longitudinal smoother area with a broken, skirt-like edge, 16–33 × 14–24 µm ($\bar{x}$ = 24.6 ± 3.6 × 17.9 ± 2.1 µm), deep orange (6A8); warts crowded, cylindrical, annulate, with flat tops, except in longitudinal smoother area, where they are broad, shallow bumps; wall hyaline; wall plus warts 1.2–2.5 µm thick. Telia in clusters of irregular size and shape, pulvinate, erumpent through epidermis, mandarin orange (6B8). Teliospores cuboid to oblong, 12.5–26 × 12.5–18 µm, wall thin, <1 µm. Basidiospores globose, subglobose, or irregular, 9–10(–12) × 8–10(–12) µm, surrounded by a mucilaginous sheath when deposited on microscope slides.

On *Picea*. Spermogonia and aecia on current-year needles, causing premature needle loss. Spermogonia amphigenous, prominent, subepidermal, 105–170 µm wide × 86–160 µm high, rusty orange or brown when dry; hymenium poorly defined, flat to concave. Spermatia ellipsoidal, 2.5–3 × 1.5–2 µm. Aecia discrete, not confluent, tubular or tongue-like, even in width, 0.3–0.5 mm, up to 3 mm long, mostly epiphyllous. Aeciospores globose, subglobose, ellipsoidal, or slightly ovoid, with a broad shallow cap at one or both ends, part of a broad longitudinal smoother area with a broken, skirt-like edge, 17–31(–36) × 14–22 µm ($\bar{x}$ = 23.5 ± 3.2 × 18.2 ± 1.7 µm), orange (6A7); warts cylindrical with thin basal connections, annulate, with flat or uneven tops, except in longitudinal smoother area, where they are broad, shallow bumps; wall hyaline, 0.8 µm thick; wall plus warts 0.8–3.3 µm thick. Peridium persistent; cells overlapping, polygonal, round or square, outer surface shallowly concave, wall smooth to slightly rough, inner surface flat or convex and covered densely with fingerlike warts, side walls narrow and striate or rugulose.

Notes

Like most telial hosts of *Chrysomyxa*, *Chamaedaphne calyculata* has evergreen leaves in which the mycelium of *C. cassandrae* overwinters. In early spring, telia form on the underside of the leaves, followed by uredinia. In Europe, telia may be rare (Sydow and Sydow 1912; Kuprevich and Tranzschel 1957), but this does not seem to be the case in North America, where telia were seen in many herbarium collections from diverse locations and on infected plants in the field. Basidiospores produced by the germinating teliospores cause infection on young needles of adjacent spruce. Abundant spermogonia form on the needles, followed by aecia, which later result in premature defoliation. Both aeciospores and urediniospores cause new infections on *Chamaedaphne calyculata*.

Inoculation experiments by Clinton (1908) and Fraser (1911, 1912) showed the connection of the aecial state, *Peridermium consimile*, on *P. mariana* and *Picea rubens* Sarg., with the uredinia and telia on *Chamaedaphne calyculata*. In the present study, *P. glauca* and *P. pungens* were inoculated with basidiospores from infected *Chamaedaphne calyculata* from north-central Alberta. These samples, in addition to Fraser's (PUR) from Nova Scotia, provided authentic material to formulate an accurate description of the spermogonia and aecia of *C. cassandrae*. The telial host and the urediniospore morphology of *C. cassandrae* are distinct from other members of the *C. ledi* complex, as defined by Savile (1950, 1955). *Chrysomyxa cassandrae* also differs from other members of the *C. Ledi* complex in the presence of a mucilaginous sheath around the basidiospores and in the large size and irregular shape of these spores. These differences would be obscured by placing *C. cassandrae* as a variety of the European *C. ledi* (Savile 1950, 1955). The aeciospores of *C. cassandrae* and *C. nagodhii* are, however, difficult to distinguish, even with SEM (Figs. 1E, 1F, 5G, and 5H), and the broad-leaved hosts of both rusts, *L. groenlandicum* and *Chamaedaphne calyculata*, may occur in the same boggy habitats. Outbreaks of spruce needle rusts in such areas will likely be a combination of both *C. cassandrae* and *C. nagodhii* as well as the epiphyllous *Ledum* rust, *Chrysomyxa ledicola* (Lindgren 1933). The subtle differences listed in Table 1 may aid in distinguishing between the aecia of *C. nagodhii* and *C. cassandrae*. In Eurasia, the larger spore size, fine tapering warts, and narrow longitudinal groove of *C. ledi* aeciospores should be adequate characters to distinguish this species from *C. cassandrae* (see mean urediniospore and aeciospore size; Figs. 2A and 2B).

Chrysomyxa cassandrae is common on spruce in the northeastern U.S.A., where it has been reported to cause severe epidemics of needle rust on *P. mariana* and *P. pungens* (Lindgren 1933; Hodson and Christensen 1942). In this study, artificial inoculation also produced severe infection of current-year needles on 8-year-old *P. pungens*, supporting previous evidence that this species is highly susceptible and may be at risk if grown in areas where *Chamaedaphne calyculata* is abundant.

Chrysomyxa chiogenis Dietel, Bot. Gaz. 19: 303. 1894. Figs. 3A–3J

≡*Melampsoropsis chiogenis* (Dietel) Arthur, N. Am. Flora, 7(2): 121. 1907.

TYPE: On *Gaultheria hispidula* (L.) Muhl. (as *Chiogenes serpyllifolia* Salisb.), Forest Co., Wisconsin, June 1893, J.J. Davis 6078, comm. Ellis (PUR 4899! Isotypes BPI 190498, NY 53850, 27734).

HOSTS AND DISTRIBUTION: Telia and uredinia have been collected on *G. hispidula* in British Columbia, Ontario, Quebec, New Brunswick, Newfoundland, and northeastern U.S.A. (New York, New Hampshire, Wisconsin). It likely has a much wider distribution. In the aecial state it is known only from inoculations conducted in Ontario on current-year needles of *P. mariana* and *P. glauca* (Faull 1936).

Description

On *Gaultheria*. Uredinia and telia hypophyllous on leaves of previous year. Uredinia scattered, circular to elliptical, 0.2–0.8 mm in diam., subepidermal, dehiscent from center, covered by a peridium of one or more layers of collapsed cells with walls 1.2–1.6 µm thick. Urediniospores globose, subglobose, or ellipsoidal, with a flat area, 15–32 × 13–21 µm ($\bar{x}$ = 21.6 ± 3.6 × 16.3 ± 1.6 µm); warts cylindrical or joined to form elongated or maze-like ridges, annulate; wall hyaline, very thin; wall plus warts 1.2–2.5 µm thick. Telia hypophyllous, subepidermal, orange, waxy, scattered, round or oval, 0.2–1 mm in diam. Teliospores catenulate, six or more in a chain, 8–19 × 7–15 µm. Basidia slightly curved

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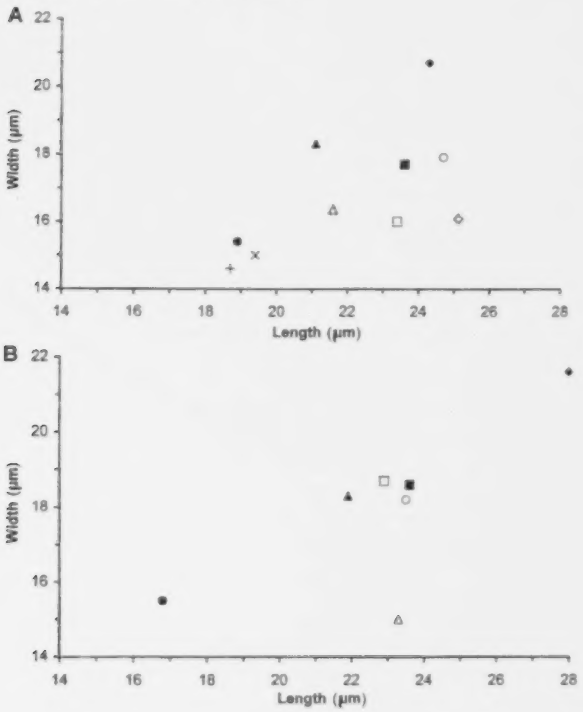
Table 1. Comparison of the spermogonial and aecial stages of *C. nagodhii* and *C. cassandrae*.

	C. nagodhii	*C. cassandrae*
Aeciospore ornamentation	Longitudinal cap slightly rough with smooth edge	Longitudinal cap with broad flat warts; edge broken and fissured
	Warts tapered, 4 annuli	Warts cylindrical, 3 annuli
Outer peridium surface	Cells deeply concave, with sharply defined edges, slightly rough surface	Cells shallowly concave with poorly defined edges, smooth to slightly rough surface
Inner peridium surface	Cells shallowly concave with a raised edge; warts shallow, irregular, discrete and fine or forming shallow ridges, sometimes appearing reticulate	Cells flat to convex; warts distinct and densely crowded, appear fingerlike; edges striate or rugulose
Spermatia	3–4.5 × 2–3.5 µm	2.5–3 × 1.5–2 µm

Fig. 2. Comparison of mean size of (A) urediniospores and (B) aeciospores of *Chrysomyxa reticulata* (●), *Chrysomyxa chiogenis* (△), *Chrysomyxa ledi* s.s. (◆) and species of *Chrysomyxa* formerly considered varieties of *C. ledi* (○, *C. cassandrae*; ▲, *Chrysomyxa neoglandulosi*; □, *Chrysomyxa nagodhii*; ■, *Chrysomyxa rhododendri*; and ◇, *Chrysomyxa vaccinii*). Note much smaller size of *C. ledi* urediniospores from Japan (×) compared with those from Europe (◆, *C. ledi* s.s.); larger size of *C. ledi* compared with *Ledum* rusts from North America; and congruence of *C. reticulata* urediniospores on *Ledum* (●) and *Rhododendron* (+). Aeciospores of *C. ledi* from Japan and *C. vaccinii* are unknown.



to strongly arched, four celled. Basidiospores subglobose, 7–9 µm in diam. (Faull 1936).

On *Picea*. Spermogonia unknown. Aecia on discolored portions of current-year needles, along stomatal lines, amphigenous, 0.5–2 mm wide. Aeciospores ellipsoidal or ovoid, ends smooth, (15)20–28 × 13–18 µm ($\bar{x}$ = 23.3 ± 2.6 × 15.0 ± 1.3 µm); warts annulate, broad and truncate with uneven tops, often joined into ridges; wall hyaline, very thin; wall plus warts 2–3.3 µm thick. Peridium delicate, shredding at apex, cells separate easily, densely warted inside, smooth outside.

Notes

An early report that this rust might be systemic in *Gaultheria* (Savile 1950) was based on misinterpretation of heavy localized infections (Savile 1955). This rust is rarely collected, probably because of the inconspicuous telial host. The natural distribution of the aecial stage is unknown because the aeciospores are similar in size to species that have been considered part of the *C. ledi* complex (sensu Savile 1950, 1955) (Fig. 2). In specimens examined from both Quebec and British Columbia, telia were abundant; therefore the aecial stage may be more common than previously thought.

Inoculated material by Faull (1936) and his colleagues was used to formulate the description of the aecial state. Two of these collections, however, are questionable because there were spermogonia present on the needles. It is possible that there was contamination from other rusts in the vicinity (some of the experiments were conducted outdoors) or that the absence of spermogonia is not a reliable feature. However, the former possibility is more likely, because the spores of the doubtful collections (BPI 190502 and 190503) were morphologically different from those found on needles without spermogonia, and an infected control was also included in the material.

Although rarely collected, *C. chiogenis* is interesting for several reasons. The absence of spermogonia is unusual within the genus and suggests that some modification has occurred to its sexual cycle (see further discussion under *C. vaccinii* and *Peridermium zilleri*). Ziller (1974) noted that the urediniospores of *C. vaccinii* are almost indistinguishable from those of *C. chiogenis*. This study shows that the spores of *C. vaccinii* are more consistently elongated than those of *C. chiogenis*, and the warts of *C. vaccinii* urediniospores are narrower and more discrete. Apart from these differences, they are very similar in morphology, including the presence of an indistinct smoother area on most urediniospores.

Also intriguing is the somewhat different morphology of the urediniospores of *C. chiogenis* from eastern (Quebec) (Fig. 3C) and western (British Columbia) Canada (Figs. 3D and 3E). In the samples from British Columbia, spores are longer (max. 32 µm compared with 25 µm); the warts are well defined and joined into long ridges at the spore ends and sometimes elsewhere; wart tops are bumpy and pitted (Figs. 3D and 3E). From Quebec (Fig. 3C), the spores are

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Fig. 3. *Chrysomyxa chiogenis*. (A) Leaf (about 1 cm long) of *Gaultheria hispidula* with scattered hypophyllous uredinia and telia (Type). (B–E) Urediniospores: (B) LM, Prince George, British Columbia; (C) SEM of single spore, Quebec; (D) SEM of single spore showing warts joined into ridges, British Columbia; and (E) surface ornamentation showing bumpy, pitted warts. (F–H) Aeciospores (from inoculation, BPI 190499): (F) LM; (G) SEM of two spores; and (H) warts with uneven tops. (I, J) Aecial peridium: (I) smooth outer surface and (J) warted inner surface. In Figs. 3B, 3C, 3D, 3F, and 3G, scale bars = 10 μm; in Figs. 3E and 3H, scale bars = 2 μm; in Figs. 3I and 3J, scale bars = 20 μm.

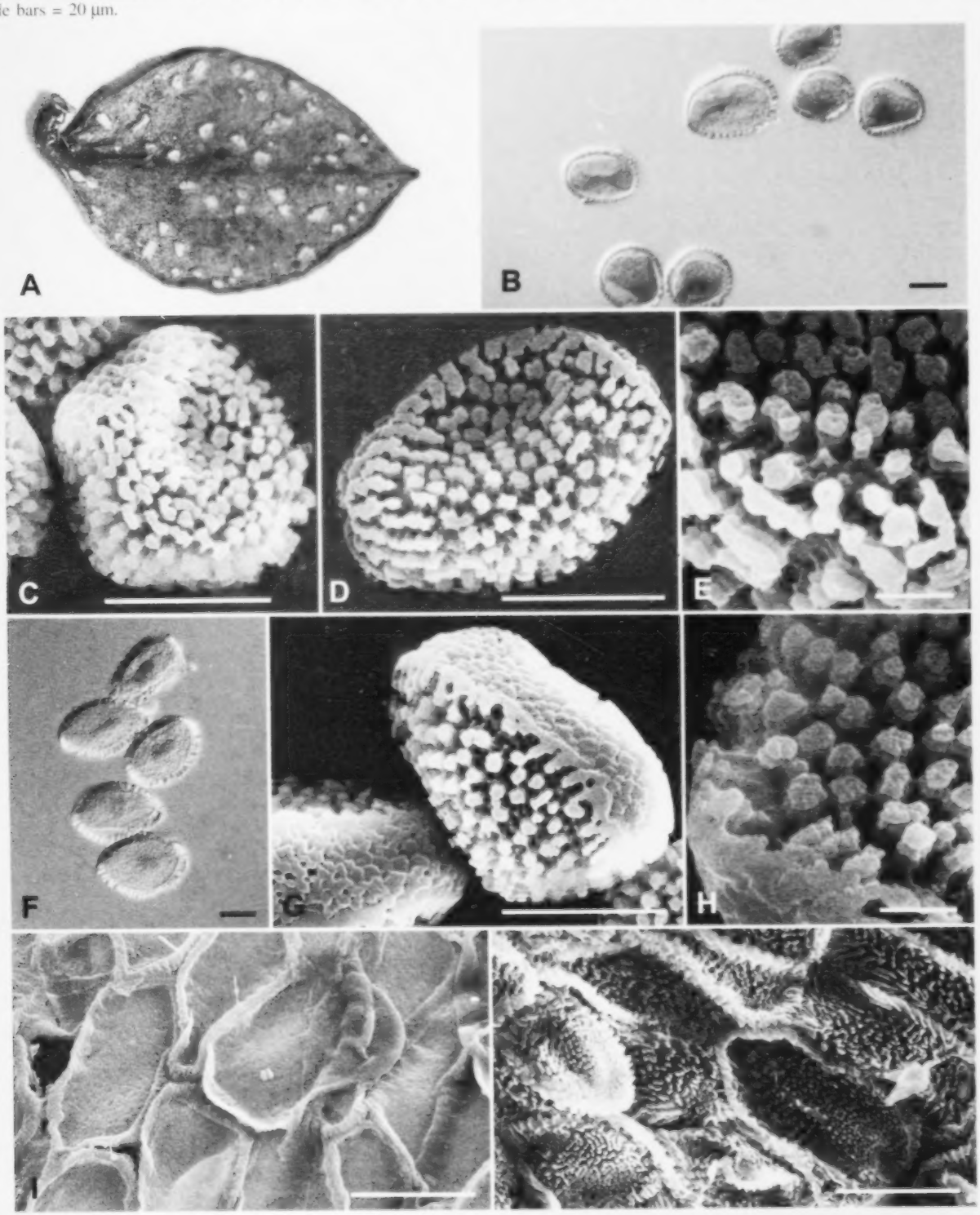

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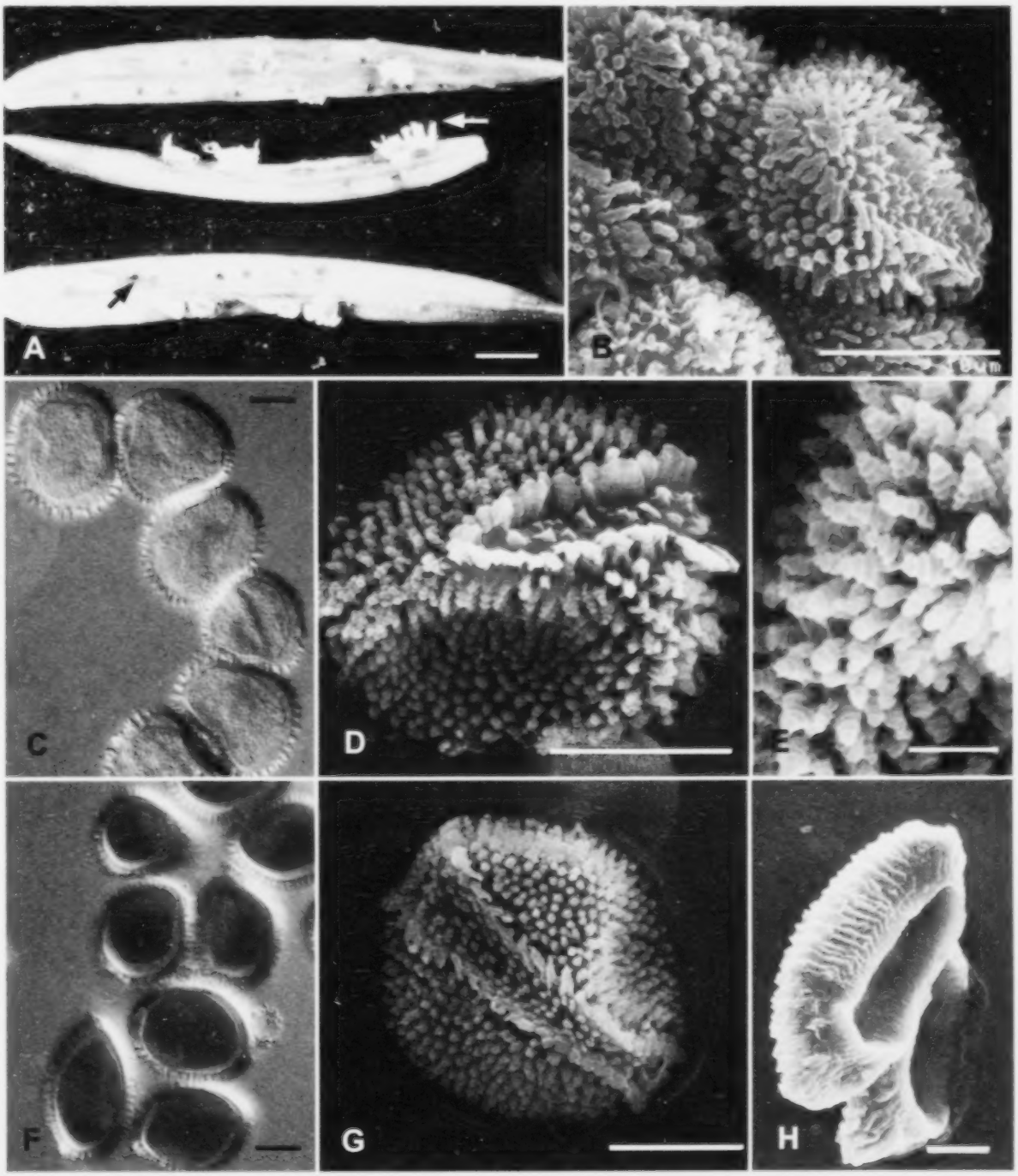
Fig. 4. *Chrysomyxa ledi*. (A) Infected needles of *Picea abies* with spermogonia (black arrow) and aecia (white arrow). Note shredding of aecial peridium. (B) SEM of urediniospores, Japan. Spores are smaller than European samples, and warts are often confluent. (C–E) Urediniospores, Europe: (C) by LM; (D) single spore with well-defined groove; and (E) narrow, tapered warts. (F, G) Aeciospores. Note narrow warted groove (G). (H) Aecial peridium, showing broad, coarsely striate side walls and concave outer surface of cells. In Fig. 4A, scale bar = 1.5 mm; in Figs. 4B–4D and 4F–4H, scale bar = 10 μm; in Fig. 4E, scale bar = 2 μm.



more rounded, warts are smoother topped, basal connections between warts are less well developed, and spores have a rough longitudinal stripe. Although they lack a reticulate area, some urediniospores from Quebec closely resemble *C. reticulata* in size, shape, and overall wart morphology. Examination of more collections is needed to determine

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Fig. 5. *Chrysomyxa nagodhii*. (A) Column of urediniospores extruded from uredinium on underside of *Ledum groenlandicum* leaf (SEM). (B) Cross section of uredinium. Note peridium of several layers of cells (arrow). (C) Cross section of telium, showing thin-walled, catenulate teliospores. (D, E) Urediniospores by LM (D) and SEM (E), showing almost-smooth surface (central Alberta, CFB 22066). (F–H) Aeciospores: (F) note small cap at ends of spores (LM); (G) smooth-edged longitudinal caplike stripe (SEM); and (H) details of surface ornamentation (on *Picea pungens*, from inoculation, CFB 22186). (I, J) Aecial peridium: (I) concave outer surface of cells and (J) warted inner surface. (K) A mite, *Dentizetes ledensis*, commonly found on infected *L. groenlandicum*, carrying urediniospores on the surface (central Alberta). In Figs. 5A and 5K, scale bars = 100 μm; in Figs. 5B–5G, scale bars = 10 μm; in Fig. 5H, scale bar = 2 μm; in Figs. 5I and 5J, scale bars = 20 μm.

whether eastern and western collections differ consistently. It should also be noted that published reports of the urediniospore size are extremely variable, from a maximum length of 29 μm (Dietel 1894) to 42 μm (Savile 1950).

Chrysomyxa ledi de Bary, Bot. Z. 37: 809. 1879. Figs. 4A–4H

≡*Chrysomyxa ledi* de Bary var. *ledi*, Can. J. Res. C, 28: 324. 1950.

=*Melampsoropsis abietina* (Alb. & Schwein.) Arthur, N. Am. Flora, 7: 119. 1907. p.p.

=*Uredo ledi* Alb. & Schwein., Consp. Fung., p. 125. 1805.

≡*Erysibe ledi* (Alb. & Schwein.) Wallr., Flora Cryptogam. Ger. II, No. 1620, p. 199. 1833.

≡*Coleosporium ledi* (Alb. & Schwein.) Schröt., in Cohn Beitr. Biol. Pflanzen, III(1): 55. 1879.

=*Caeoma ledi* Link, Willdenow, Spec. Plant. Gen. VI, 2, p. 15. 1825. [*fide* Saccardo 1888].

=*Caeoma ledi* Schltdl., Flora Berol. II: 122. 1824.

=*Caeoma piceatum* Link, in Linn. Spec. Plant. II, pp. 62–63. 1825. p.p.

=*Uredo ovoideo-aurantiaca* Bonord., Coniom. Cryptom., p. 32. 1860. [*fide* Saccardo 1888].

=*Uredo abietina* Spreng., Syst. Veg. IV, p. 572. 1827. [*fide* von Thümen 1880].

=*Pucciniastrum ledi* Karst., Bidr. Känned. Finlands Nat. Folk, 31: 57. 1879. [*fide* Sydow and Sydow 1915].

=*Aecidium abietinum* Alb. & Schwein., Consp. Fung., p. 120. 1805. p.p.

≡*Peridermium abietinum* (Alb. & Schwein.) Thüm., Mitt. Forstl. Versuchswesen Oesterr. 2: 320–321. 1880.

TYPE: On *Ledum palustre* L., Grunewald near Berlin, Germany.

HOSTS AND DISTRIBUTION: *Chrysomyxa ledi* occurs in Eurasia throughout the range of its broad-leaved hosts, independent of host alternation: in northern Europe, on *L. palustre* (*Rhododendron tomentosum* Harmaja); in Siberia, on *Ledum hypoleucum* Kom. (*Rhododendron hypoleucum* (Kom.) Harmaja) and *Ledum macrophyllum* Tolm. (*Rhododendron tolmachevii* Harmaja) (Azbukina 1974); and in Japan, on *L. palustre* ssp. *diversipilosum* Hara (Hiratsuka et al. 1992). The aecial stage is found on native and ornamental spruces: in Europe, on *P. abies*, *P. engelmannii*, *P. glauca*, *Picea obovata* Ledebour, *P. mariana*, and probably others (Hylander et al. 1953; Kuprevich and Tranzschel 1957; Gjaerum 1974); in Siberia, on *Picea ajanensis* Fisch. (Azbukina 1974); in China, on *Picea likiangensis* (Franchet) Pritzel (Spaulding 1961); and in Japan, on *Picea jezoensis* Carr. (Hiratsuka et al. 1992) and *Picea glehnii* (Fr. Schmidt) Masters (Ono and Isono 1992).

Description

On *Ledum*. Uredinia and telia hypophyllous on leaves of previous year, uredinia occasionally caulicolous. Uredinia circular, 0.2–0.3 mm wide, single or in groups, with a peridium of 2–3 layers of thin-walled pseudoparenchymatous cells that are much smaller than spores. Urediniospores globose, subglobose, or ovoid, occasionally ellipsoidal, 18–30 × 16–26 μm ($\bar{x}$ = 24.2 ± 1.7 × 20.7 ± 1.3 μm), sometimes notched or flattened at one end because of a narrow longitudinal groove with or without a well-defined edge; wall hyaline, 0.5–0.8 μm thick; wall plus warts, 2.5–2.9 μm thick. Telia sparsely aggregated, flat, blood red to orange–red. Teliospores oblong to cuboid, 13–30 × 10–20 μm (Saccardo 1888; Sydow and Sydow 1915; Kuprevich and Tranzschel 1957). Basidiospores ovoid, 11 × 7 μm (Saccardo 1888).

On *Picea*. Spermogonia and aecia on current-year needles. Spermogonia amphigenous, subepidermal; in cross section, hymenium concave to slightly flattened, 100–190 μm wide × 90–150 μm high. Spermatia ovoid, subglobose, or globose, 1.2–2 × 1.2–1.6 μm. Aecia amphigenous, tubular, 0.3–1.3 mm wide. Aeciospores ovoid, ellipsoidal, globose, or subglobose, 20–38 × 15–28 μm ($\bar{x}$ = 28.0 ± 4.1 × 21.6 ± 2.4 μm), with a distinct narrow longitudinal groove; warts crowded, annulate, tapering; wall hyaline, 0.8 μm thick; wall plus warts 1.6–4.9 μm thick. Peridium dehiscing at apex, later shredding, leaving a fringe around sorus; outside of cells deeply concave, more or less smooth; inside of cells shallowly concave, shallowly and densely warted, warts often arranged in undulating rows; lateral margins broad (3–6 μm or more) with coarse striations.

Notes

Chrysomyxa ledi, the Eurasian hypophyllous *Ledum* rust, is distinct in morphology from the rusts occurring on *Ledum* in North America. SEM clearly demonstrates the morphological differences, especially of the aeciospores and urediniospores, distinguishing *C. ledi* s.s. from the North American species, described herein as *C. nagodhii* and *C. neoglandulosi* (see Notes and Figures under those species). The aeciospores of *C. ledi* are also somewhat larger than the aeciospores of the North American species (Fig. 2). Five specimens from Japan (PUR) were examined on several varieties of *L. palustre* (now all considered *L. palustre* ssp. *Diversipilosum* (Hiratsuka et al. 1992)); they also differ somewhat from the European specimens, and therefore were not used to compile the species description. Their urediniospores are smaller (14–25 × 11–21 μm, $\bar{x}$ = 19.4 ± 2.7 × 14.9 ± 2.2 μm) than the European samples and their surface ornamentation variable (Figs. 4B and 4D). Warts have broad irregular tops, and spores may have a flattened end where warts are confluent; however, there is seldom a well-defined groove. A thorough investigation of the

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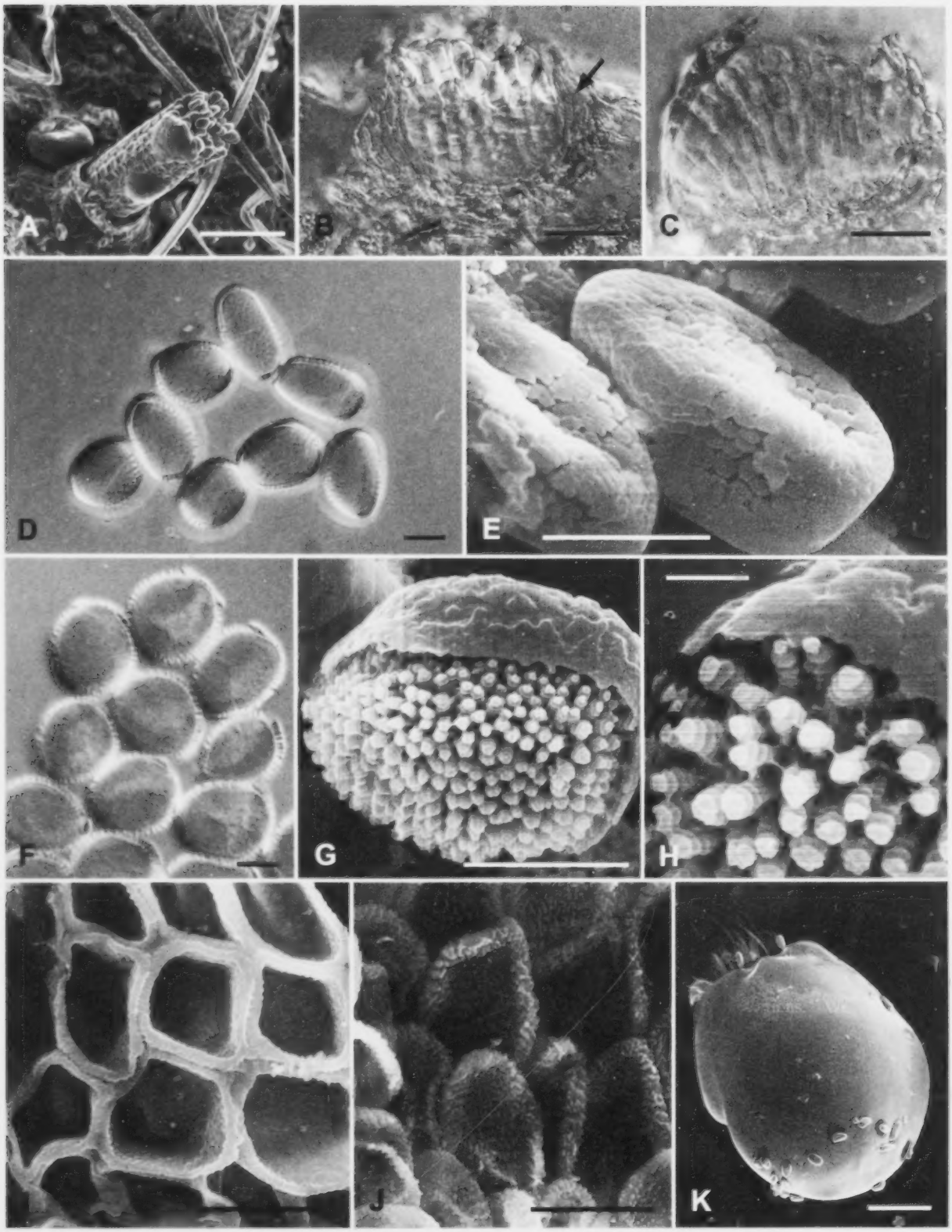

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Fig. 6. *Chrysomyxa neoglandulosi*. (A) Leaf spots (arrows) on infected *Ledum glandulosum* adjacent to *Picea engelmannii* (lower left), type locality, Waterton, Alberta. (B) Cross section of leaf with uredinium. (C–E) Globose urediniospores: (C) by LM; (D) single spore (SEM); and (E) very fine, almost echinulate warts. (F–H) Aeciospores: (F) by LM; (G, H) showing very fine, narrow warts with annuli barely visible (SEM). (I, J) Aecial peridium: (I) concave, densely rugose outer surface of cells, with coarsely striate margins where cells join (arrow); and (J) inner surface with shallow, ridgelike ornamentation. In Fig. 6B, scale bar = 100 μm; in Figs. 6C, 6D, 6F, and 6G, scale bars = 10 μm; in Figs. 6E and 6H, scale bars = 2 μm; in Figs. 6I and 6J, scale bars = 20 μm.

hypophyllous rusts on *Ledum* and *Rhododendron* in Japan is needed to determine whether they should be considered separate species from rusts on the same host genera elsewhere (see also Notes under *C. rhododendri*).

de Bary (1879) proved, experimentally, the connection between the telial stage of *C. ledi* on *L. palustre* and the aecial stage on spruce, and he detailed the differences between *C. ledi* and *C. rhododendri*. The coarser margins of the peridial cells of *C. ledi* (Fig. 4H) are an important distinguishing feature between the aecial stages of the two rusts in Europe. Although *C. ledi* is not known to occur in North America, certain morphological features of *Ledum* rusts from both continents suggest a common ancestor. The peridial cells of *C. ledi* are remarkably similar to those of *C. ledicola* in North America (Crane 2000), and the peridium of both species shreds in a similar manner during aeciospore release (Fig. 4A). Western and coastal variants of *C. ledicola* are also sometimes similar in aeciospore and urediniospore size to *C. ledi* and may possess an indistinct groove (Crane 2000). Although *C. ledicola* is chiefly epiphyllous on its *Ledum* host, it is occasionally hypophyllous. The coarse peridial cells of *C. neoglandulosi* and the fine-tapered warts on the spores (Fig. 6) also suggest phylogenetic affinity with *C. ledi*; both aeciospores and urediniospores of *C. neoglandulosi*, however, are considerably smaller (Fig. 2).

The occurrence of *C. ledi* and the systemic species *Chrysomyxa woroninii* Transzschel on the same host plants has, in the past, led to the conclusion that they are different states of the same fungus (Liro 1907). Field observations and inoculation experiments have confirmed that they are different species that produce different signs and symptoms on both hosts, *Ledum* and *Picea* (Tranzschel 1903; Crane et al. 2000).

In northern Europe, rainy summers favor heavy infection of spruce by *C. ledi* (Melekhov 1946). Trees over large areas may turn bright yellow. Premature shedding of needles probably affects incremental growth.

Chrysomyxa nagodhii P.E. Crane, sp.nov. Figs. 5A–5K

=*Chrysomyxa ledi* de Bary var. *groenlandici* Savile, Can. J. Bot. 33: 490. 1955. [nom.nud.; telia not described]

=*Melampsoropsis abietina* Arthur, N. Am. Flora, 7: 119. 1907, p.p.

TYPE: On *Ledum groenlandicum* Oeder (*Rhododendron groenlandicum* (Oeder) Kron & Judd), near Obed Summit, Hwy. 16, E of Range Rd. 221, Alberta, P.E. Crane (Holotype DAOM, Isotypes DAVFP, PUR, CFB 22207).

ETYMOLOGY: Named for nagodhi, an aboriginal (Chipewyan) name for the major telial host, *L. groenlandicum*.

HOSTS AND DISTRIBUTION: This species probably occurs throughout the range of *Ledum decumbens* (Ait.) Lodd. ex Steud. (*Rhododendron subarcticum* Harmaja) and *L. groenlandicum* in North America, independent of host alternation. This includes Nova Scotia to British Columbia, the Yukon and Northwest Territories, and Alaska, south to Connecticut, Michigan, New Hampshire, New York, and Wisconsin. One collection on *Rhododendron* sp. from Whalley, B.C., reported as *C. ledi* var. *rhododendri*, was reidentified as *C. nagodhii*. The aecial state has been verified on *P. engelmannii*, *P. glauca*, *P. mariana*, *P. pungens*, and *P. rubens*. Collections identified as *C. ledi* on *P. sitchensis* have so far proven to be inconsistent with *C. nagodhii* (see Notes under *C. vaccinii* and *Peridermium zilleri*). The identity of many previous North American records (as *C. ledi* or *C. ledi* var. *groenlandici*) on spruce is in doubt because of confusion with species of similar spore size, including *C. cassandrae*, *C. chiogenis*, and the small-spored western North American form of *C. ledicola* (Crane 2000).

Description

In *Ledo* vel *Rhododendro*. Uredinia et telia hypophylla in foliis anni superioris, maculas flavas et aurantiacas efficientia. Uredinia 0.3 mm lata, cupulata, cum peridio incohato. Urediniosporae ellipsoideae, ovoideae, subglobosae, vel irregulares, truncatae in extremo altero vel utroque, 15–36 × 12–22 μm ($\bar{x}$ = 23.4 ± 3.2 × 16.0 ± 2.1 μm), meloni-flavae; tunica levis prope extrema sporae, sed in lateribus cum verrucis humilibus, dense congregatis, indistinctis, in summo planis et magnitudine et forma variis; tunica cum verrucis 0.8–2.5 μm crassa. Telia valde aurantiaca, discreta, gelatinosa, 0.1–0.2 mm lata. Teliosporae cuboideae, ellipticae quando maturant, lateriores ad summum sori, 12–23 × 15–28 μm. Basidiosporae globosae ad subglobosae cum apiculo parvo, et magnitudine et forma irregulares, 6–13 × 6–12 μm.

In *Picea*. Spermogonia et aecia in lineis distinctis et rubigo-flavis in acubus arboreis huius anni. Spermogonia amphigena, prominens, rubigo-brunnea quando exsiccata, per mediam partem magis vel minus globosa, hymenio concavo ad aliquantum plano, 70–200 μm latum × 60–163 μm altum. Spermatia ellipsoidea, aliquando globosa, 3–4.5 × 2–3.5 μm. Aecia amphigena, 0.25–2 mm lata, tubularia, separata. Aeciosporae forma et magnitudine variae, globosae, subglobosae, ellipsoideae vel ovoideae, cum tegimento humili in extremo altero vel utroque, pars lineae longitudinalis et leviter-marginatae per latus alterum sporae, 15–31(–34) × 14–24 μm ($\bar{x}$ = 22.9 ± 3.1 × 18.7 ± 2.1 μm), valde aurantiacae, tunica hyalina, <0.8 μm crassa; verrucae congregatae, fastigatae, latitudine variae, annulatae, superficies tegamenti prope levis; tunica cum verrucis 1.6–4.1 μm crassa. Peridium scindet in maturitate, cellulae facile separant; superficies externa cellulae alte concava, cum marginibus distinctis, tunica rugulosa; superficies interna cellulae paulo concava cum margine elevata, verrucae humiles, irregulares, discretae et leves vel dorsa humilia formantes, aliquando reticulatae videntur.

On *Ledum* or *Rhododendron*. Uredinia and telia hypophyllous on leaves of previous year, causing a yellow and

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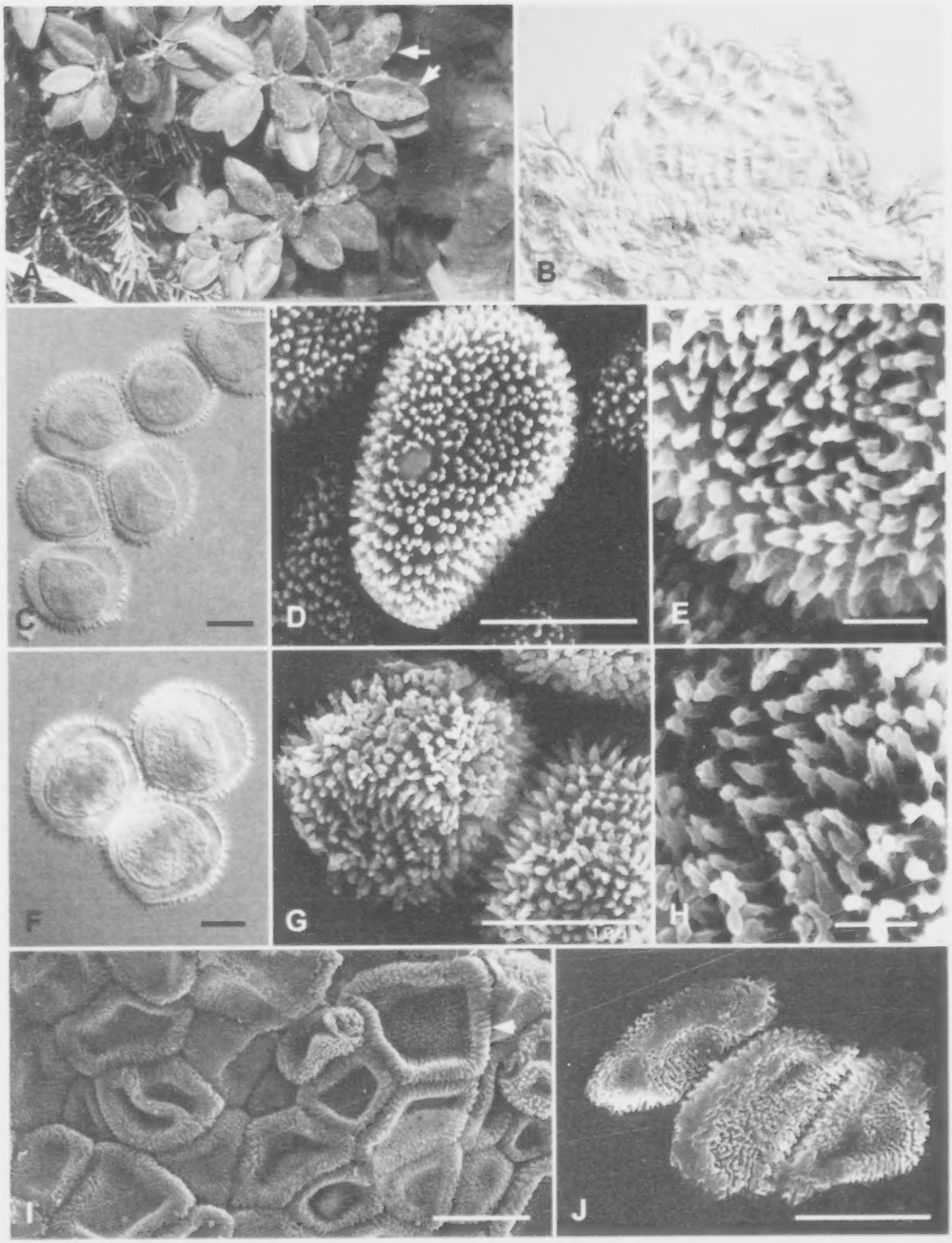

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orange mottling. Uredinia 0.3 mm wide, cupulate, with a rudimentary peridium. Urediniospores ellipsoidal, ovoid, subglobose, or irregular, with one or both ends truncate, 15–36 × 12–22 µm ($\bar{x}$ = 23.4 ± 3.2 × 16.0 ± 2.1 µm), melon yellow (5A6); wall smooth at ends of spore, but with shallow, closely crowded, indistinct, flat-topped warts of variable size and shape on sides; wall plus warts 0.8–2.5 µm thick. Telia deep orange (5A8 or 6A7), discrete, gelatinous, 0.1–0.2 mm wide; seen in cross section, hymenium is flat. Teliospores cuboid, becoming elliptical as they mature, wider toward top of sorus, 12–23 × 15–28 µm. Basidiospores globose to subglobose with a small apiculus, irregular in size and shape, 6–13 × 6–12 µm.

On *Picea*. Spermogonia and aecia on distinct rusty yellow bands on current-year needles. Spermogonia amphigenous, prominent, rusty brown when dry; in cross section more or less globose, hymenium concave to somewhat flattened, 70–200 µm wide × 60–163 µm high. Spermatia ellipsoidal, occasionally globose, 3–4.5 × 2–3.5 µm. Aecia amphigenous, 0.3–2 mm wide, tubular, separate. Aeciospores variable in shape and size, globose, subglobose, ellipsoidal, or ovoid, with a shallow cap at one or both ends, part of a smooth-edged longitudinal cap along one side of spore, 15–31(–34) × 14–24 µm ($\bar{x}$ = 22.9 ± 3.1 × 18.7 ± 2.1 µm), deep orange (5A8); wall hyaline, <0.8 µm thick; warts crowded, tapered, variable in width, annulate, surface of cap nearly smooth; wall plus warts 1.6–4.1 µm thick. Peridium shreds at maturity, cells separate easily; outer cell surface deeply concave, with sharply defined edges, wall rugulose; inner cell surface shallowly concave with a raised edge, warts shallow, irregular, discrete and fine or forming shallow ridges, sometimes appearing reticulate.

Notes

Although this North American hypophyllous *Ledum* spruce rust has been considered conspecific with the European *C. ledi*, the different *Ledum* host species and distinct morphology, especially of the aeciospores and urediniospores, support separate species status. Savile (1950, 1955) observed slight morphological differences between the European and North American forms and placed *C. nagodhii* as a variety of *C. ledi*, but because he did not describe telia, the variety name is considered invalid. The almost-smooth appearance of the urediniospores (Figs. 5D and 5E) of *C. nagodhii* is unique within the genus and very different from the evenly warted, grooved spores of *C. ledi* (Fig. 4D). Similarly, the smooth cap-like stripe of *C. nagodhii* aeciospores (Fig. 5G) differs from the well-defined narrow warted groove seen in *C. ledi* aeciospores (Fig. 4G). *Chrysomyxa nagodhii* is an exception to the "rule" that in *Chrysomyxa* the morphology of the aeciospores and urediniospores of a given species is almost identical (Savile 1950).

The telia of *C. nagodhii* appear in the early spring, followed by the uredinia, which may be present throughout the growing season. The yellow-orange leaf mottling produced by this rust on *L. groenlandicum* differs from the deep reddish discoloration induced by *C. ledicola*. This rust fungus often occurs on the same spruce trees, and even the same needles, as *C. ledicola*, but has a more sporadic occurrence than the latter. In such cases, even under a dissecting microscope, the smaller spore size, paler orange color, and more persistent peridium of *C. nagodhii* are helpful in distinguishing the two species. Distinguishing *C. nagodhii* from *C. cassandrae* in the aecial stage is much more difficult, and the broad-leaved hosts, *Ledum* and *Chamaedaphne*, occupy very similar boggy habitats. The subtle differences in their aecial characters are listed in Table 1.

The connection between the telial stage on *L. groenlandicum* and the aecial stage on spruce was proven, experimentally, by Fraser (1911, 1912) and Arthur (1912) and confirmed during this study. Fraser's inoculated material on *P. rubens* and from this study on *P. mariana* and *P. pungens* were compared and used to compile the species description.

The distinct morphology of the urediniospore surface of *C. nagodhii* suggests a dispersal mechanism that is unusual for the genus. The spore surface is sticky and the spores are extruded in long columns that remain intact if undisturbed (Fig. 5A). Brown-bodied oribatid mites, frequently observed among the uredinia on freshly collected *L. groenlandicum* leaves in central Alberta, carry urediniospores of *C. nagodhii* on their body surface (Fig. 5K). These mites have been described as a new species, *Dentizetes ledensis* V.M. Behan-Pelletier (Acari: Oribatida: Ceratozetidae) (Behan-Pelletier 2000), and have also been found in Ontario, Wisconsin, and Newfoundland, suggesting that they occur throughout the range of *L. groenlandicum* in North America. It is possible that they play a role in the dispersal of this fungus on the broad-leaved host.

Planting of cultivated rhododendrons close to areas with infected *L. groenlandicum* is not recommended because of the ability of this rust to infect these closely related host plants.

Chrysomyxa neoglandulosi P.E. Crane, sp.nov.

Figs. 6A–6J

=*Chrysomyxa ledi* de Bary var. *glandulosi* Savile, Can. J. Bot. 33: 489. 1955. [nom.nud.; telia not described]

=*Melampsoropsis abietina* Arthur, N. Am. Flora, 7: 119–120. 1907. p.p.

TYPE: On *Ledum glandulosum* Nutt. (*Rhododendron neoglandulosum* Harmaja), Waterton Lakes Natl. Park, start of trail to Little Akamina L., near Cameron L., Alberta, 11 Jul 1998, P.E. Crane (Holotype DAOM; Isotypes PUR, DAVFP, CFB 22174).

ETYMOLOGY: Named for the telial host plant, *L. glandulosum*.

HOSTS AND DISTRIBUTION: *Chrysomyxa neoglandulosi* likely occurs wherever its telial host, *L. glandulosum*, is found. This upright shrub is found in moist to wet meadows and forests in the montane to subalpine zones of southern British Columbia east of the Coast–Cascade mountains, to southwestern Alberta, southward to Montana, Idaho, Wyoming, and northern California (Douglas et al. 1999). The only reported aecial host, *P. engelmannii*, occurs in similar mountainous habitats in western Canada and U.S.A. According to Gould (1966), *C. neoglandulosi* can also attack rhododendrons.

Description

In *Ledo*. Uredinia et telia hypophylla in locis chloroticis in foliis anni superioris, vel caulicola. Uredinia <0.3 mm diam., sparsa vel in circulis, conicalia dum non aperta, cum peridio inconspecto de cellulis irregularibus et tenuiter tunicatis. Urediniosporae globosae vel subglobosae, non-

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numquam ellipsoideae, 14–28 × 11–23 µm ($\bar{x}$ = 21.1 ± 2.1 × 18.3 ± 2.3 µm), aurantiacae, tunica hyalina, distincte formata, 0.8–1.6 µm crassa; verrucae magnitudini similes, levissimae et angustae, ad spiculum fastigatae, annulationes inconspectae, coniunctiones basales inter verrucas absunt vel parvum evolutae; tunica cum verrucis 1.6–3.3 µm crassa. Telia rotunda vel elliptica, ampliora et magis irregularia quam uredinia, 0.3–0.8 mm longa, pruno-armeniaco-flava. Teliosporae 12–15 × 18–22 µm. Basidiosporae ovoideae, subglobosae, globosae, vel irregulariter formatae, cum apiculo lato, 6–10 × 6–9 µm.

In *Picea*. Spermogonia et aecia in acuibus arboreis huius anni. Spermogonia amphigena, elliptica, pallide-brunnea; per mediam partem, 90–170 µm alta × 114–144 µm lata, hymenium planum vel tenuiter concavum, cum margine tenui et fusca et distincte formata. Spermatia ellipsoidea vel ovoidea, 2.5–3.7 × 1.6–2.5 µm. Aecia amphigena, discreta. Aeciosporae globosae ad subglobosae, ellipsoideae vel ovoideae, 18–25 × 14–22 µm ($\bar{x}$ = 21.9 ± 1.6 × 18.3 ± 2.2 µm), fusco-aurantiacae; tunica hyalina, 1.6–2.5 µm crassa, verrucae parvissimae, fere echinulatae, congregatae, annulationes inconspectae; tunica cum verrucis 1.6–3.0 µm crassa. Peridium simile tubo, persistens; superficies externa cellularum concava, dense rugosa, cum marginibus late et crasse striatus; superficies interna plana ad exigue concava, cum ornamentis paulis et dorso similibus.

On *Ledum*. Uredinia and telia hypophyllous on chlorotic spots on leaves of previous year, or caulicolous. Uredinia <0.3 mm in diameter, scattered or in circular groups, conical when unopened, erumpent through epidermis, with an inconspicuous peridium of irregular thin-walled cells. Urediniospores globose or subglobose, occasionally ellipsoidal, 14–28 × 11–23 µm ($\bar{x}$ = 21.1 ± 2.1 × 18.3 ± 2.3 µm), orange (6B8 or 6A8); wall hyaline, well defined, 0.8–1.6 µm thick; warts even in size, very fine and narrow, tapering to a point, annuli very faint and only visible by SEM, basal connections between warts absent or poorly developed; wall plus warts 1.6–3.3 µm thick. Telia round or elliptical, larger and more irregular than uredinia, 0.3–0.8 mm long, apricot-yellow (5B6). Teliospores 12–15 × 18–22 µm. Basidiospores ovoid, subglobose, globose, or irregular in shape, with a broad apiculus, 6–10 × 6–9 µm.

On *Picea*. Spermogonia and aecia on current-year needles. Spermogonia amphigenous, elliptical, pale brown; in cross section, 90–170 µm high × 114–144 µm wide, hymenium flat or slightly concave, with a well-defined, thin dark margin. Spermatia ellipsoidal or ovoid, 2.5–3.7 × 1.6–2.5 µm. Aecia amphigenous, discrete. Aeciospores globose to subglobose, ellipsoidal or ovoid, 18–25 × 14–22 µm ($\bar{x}$ = 21.9 ± 1.6 × 18.3 ± 2.2 µm), dark orange (5A8); wall hyaline, 1.6–2.5 µm thick, warts very tiny, almost echinulate, crowded, annuli difficult to discern; wall plus warts 1.6–3.0 µm thick. Peridium tubelike, persistent; outer surface of cells concave, densely rugose, with wide coarsely striate margins; inner surface flat to slightly concave, with shallow ridge-like ornamentation.

Notes

Chrysomyxa neoglandulosi was first distinguished from *C. ledi* and from other North American hypophyllous rusts on *Ledum* spp. by Savile (1950, 1955), who designated it as a variety of the European rust. However, because he did not describe the telia, the variety name is invalid and this rust has continued to be called *C. ledi*. The smaller, more globose spores, the different broad-leaved host species, and the much finer ornamentation of both the urediniospores and aeciospores (Figs. 6C–6H) clearly distinguish it from other rusts of the *C. ledi* complex and support separate species status. Two young *P. engelmannii* were inoculated in 1998 with basidiospores from *L. glandulosum* collected at Waterton, Alberta. After 10 d, two needles formed spermogonia, but they failed to develop aecia. Two other spruce collected very close to (almost touching) infected *L. glandulosum* were brought to Edmonton, Alberta, to observe development of any infection already present; other potential sources of infection, such as *L. groenlandicum*, could not be found in the vicinity of the collected spruce. These trees developed both spermogonia and aecia that were consistent with other purported samples of *C. neoglandulosi*. The similarity of the aeciospores to the urediniospores in size, shape, and surface ornamentation (Figs. 6C–6H) leaves little doubt that this is the aecial state of *C. neoglandulosi*.

Chrysomyxa neoglandulosi probably survives in the uredinial state on *L. glandulosum* in the absence of *P. engelmannii*, and telia may not form in certain locations (Krebill 1968). Uredinia are found throughout the growing season on leaves of the previous year, which are later shed. Current-year leaves become infected, but rarely show signs of infection until the next spring, when uredinia, or telia followed by uredinia, form from overwintered mycelium within the leaves (Krebill 1968). In late spring, basidiospores produced by germinating teliospores on *L. glandulosum* infect current-year needles of *P. engelmannii*.

Chrysomyxa neoglandulosi and *C. ledicola* are the only species of *Chrysomyxa* in North America that do not have aeciospores or urediniospores consistently marked by a longitudinal groove or cap. In both species, the spores are more often globose than elongate, and they have aecial peridial cells with broad, coarsely striate side walls (Crane 2000). However, these species are unlikely to be confused on spruce because *C. neoglandulosi* has much smaller aeciospores than does *C. ledicola*. The extremely fine surface ornamentation of both urediniospores and aeciospores of *C. neoglandulosi* is also unique. Whereas most other North American species have warts with annuli visible by light microscopy (Crane 2000), the processes on the walls of *C. neoglandulosi* spores are finely tapered and appear almost echinulate (Figs. 6E and 6H). Under SEM, however, the indistinct annuli can be seen on the aeciospores (Fig. 6H). This species is also unusual in having peridial cells with a densely ornamented outer surface (Fig. 6I), rather than the nearly smooth surface characteristic of most of the species studied.

Chrysomyxa reticulata P.E. Crane, sp.nov. Figs. 7A–7I

=*Chrysomyxa ledi* var. *rhododendri* (de Bary) Savile, Can. J. Bot. 33: 491. 1955. p.p.

TYPE: Tunnel Trail, S of Ribbon Cr. Trail, Kananaskis, Alberta, 1 Jun 1998, P.E. Crane (Holotype DAOM; Isotypes PUR, DAVFP, CFB 22183).

ETYMOLOGY: Named for the reticulate ornamentation on part of the urediniospores.

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Fig. 7. *Chrysomyxa reticulata*. (A) Urediniospores of *C. reticulata* and *C. nagodhii* (arrow) found on the same *Ledum* leaf (Nova Scotia, PUR 4866). (B–E) Globose to subglobose urediniospores: (B) by LM and (C) by SEM, showing reticulate area on one side (from *L. groenlandicum*, northern Alberta, CFB 7334); (D) from cultivated *Rhododendron* sp. (Washington, PUR 54533); (E) details of reticulate area (left) and warts (right) with broad uneven tops. (F, G) Aeciospores from artificial inoculation of *Picea glauca*: (F) spores with longitudinal smoother stripe having a central groove (arrow); (G) details of surface ornamentation. (H) Cell of aecial peridium (arrow), among aeciospores, showing concave outer surface. (I) Shallowly concave, rugose inner surface of peridial cells. In Figs. 7A, 7B, and 7H, scale bars = 20 μm; in Figs. 7C, 7D, 7F, and 7I, scale bars = 10 μm; in Figs. 7E and 7G, scale bars = 2 μm.

HOSTS AND DISTRIBUTION: This rust has been found on *L. groenlandicum* and *L. decumbens* in both eastern (Nova Scotia) and western (Alberta, British Columbia) Canada, and the northeastern (Wisconsin) and northwestern (Washington, California) U.S.A. In Washington and California it has infected cultivated rhododendrons in nurseries. The aecia are so far known only from artificial inoculation of *P. glauca*.

Description

In *Ledo* et *Rhododendro*. Uredinia et telia hypophylla in foliis anni superioris. Uredinia in circulis, circularia, <0.1–0.5 mm lata, per mediam partem fere globosa, cum peridio delicato et inconspicuo de una propagine vel duabus cellularum irregularium vel leviter tunicatarum. Urediniosporae globosae ad subglobosae, aliquando ellipsoideae vel ovoideae, 15–24(–26) × 12–21 μm ($\bar{x}$ = 18.8 ± 2.2 × 15.4 ± 1.7 μm), pallide aurantiacoflavae, mox ad album pallescentes; tunica hyalina, levissima, 0.4–0.8 μm; verrucae separatae, congregatae, cylindricae, altitudine aequa, annulatae, cum summis latis et inaequalibus; latus alterum sporae velatum ab area longitudinali, lata, reticulata; tunica cum verrucis 0.8–2.5 μm crassa. Telia cerea, pulvinata, subepidermalia, fusciora quam uredinia, aurantiaca, rare confluentia, circularia, 0.2–0.3 mm diam., per mediam partem lenticularia. Teliosporae catenulatae, cuboideae ad oblongae, 12–19 × 8–12 μm, cum tunica levi et hyalina, <0.8 μm. Basidiosporae ellipsoideae, subglobosae vel globosae, cum apiculo exiguo et angusto, 5–8 × 5–8 μm.

In *Picea*. Spermogonia et aecia in acuibus arboreis huius anni. Spermogonia amphigena, subepidermalibus, pallide aurantiaca ad auro-brunnea; per mediam partem plus (minus) globosa, 100–110 μm lata × 80–130(–150) μm alta. Aecia amphigena, parvissima. Aeciosporae globosae ad subglobosae, saepe cum extremo plano, pars tegamenti levis et longitudinalis cum centro concavo, 15–18(–21) × 14–18 μm ($\bar{x}$ = 16.8 ± 1.4 × 15.5 ± 1.0 μm), clare aurantiacae; tunica hyalina, tenuis; tunica cum verrucis 1.6–2.5 μm crassa. Peridium tenuissimum et delicatum, non persistens; cellulae imminentes, multo largiores quam sporae, 34 × 30 μm, facile separant, in externa parte concavae et leves, in parte interna paulo concavae et rugosae.

On *Ledum* and *Rhododendron*. Uredinia and telia hypophyllous on leaves of previous year. Uredinia in groups, erumpent through the epidermis, circular, <0.1–0.5 mm wide, in cross section almost globose, with a delicate, inconspicuous peridium of one or two layers of irregularly shaped, thin-walled cells. Urediniospores globose to subglobose, occasionally ellipsoidal or ovoid, 15–24(–26) × 12–21 μm ($\bar{x}$ = 18.8 ± 2.2 × 15.4 ± 1.7 μm), pale yellow orange, soon fading to white; wall hyaline, very thin, 0.4–0.8 μm; warts separate, crowded, cylindrical, even in height, annulate, with broad, uneven tops; one side of spore covered by a broad longitudinal reticulate area; wall plus warts 0.8–2.5 μm thick. Telia waxy, pulvinate, subepidermal, darker than uredinia, orange (5B8), seldom confluent, circular, 0.2–0.3 mm in diam., in cross section lenticular. Teliospores catenulate, cuboid to oblong, 12–19 × 8–12 μm, with a thin hyaline wall, <0.8 μm. Basidiospores ellipsoidal, subglobose or globose, with a tiny narrow apiculus, 5–8 × 5–8 μm.

On *Picea*. Spermogonia and aecia on current-year needles. Spermogonia amphigenous, subepidermal, pale orange, darkening to golden brown with age; in cross section more or less globose, 100–110 μm wide × 80–130(–150) μm high. Aecia amphigenous, very small. Aeciospores globose to subglobose, often with one flat end, part of a smoother longitudinal stripe with a central groove, 15–18(–21) × 14–18 μm ($\bar{x}$ = 16.8 ± 1.4 × 15.5 ± 1.0 μm), light orange (5A5); wall hyaline, thin; wall plus warts 1.6–2.5 μm thick. Peridium very thin and delicate, not persistent; cells overlapping, much larger than spores, 34 × 30 μm, separating easily, on outside concave and smooth, on inside shallowly concave and rugose.

Notes

Chrysomyxa reticulata has the smallest spores of any known species in the genus (Crane 2000). In addition to North American and European species, spore size was compared with records of Asian species to confirm that this newly found rust did not originate there. *Chrysomyxa reticulata* was first found on a specimen of *L. groenlandicum* from Nova Scotia (PUR 4866). Although most uredinia on the leaves of this sample were of *C. nagodhii*, a few pustules on one leaf petiole bore smaller spores with different surface ornamentation. Both uredinia and telia were seen on a sample of the same host from Wisconsin collected in 1893. The early date of this collection and the widespread distribution (see Specimens examined), including locations in northern and western Alberta and northern British Columbia, far from introduced rhododendrons, suggest that *C. reticulata* is native to North America. It was likely overlooked earlier because of its occurrence on the same host as *C. nagodhii*. Although *C. reticulata* appears to be a minor component of the rust flora on *Ledum* spp., its recognition is horticulturally important because it occurs on cultivated rhododendrons. It has been assumed that the first outbreaks of rust on cultivated rhododendrons on the west coast of North America during the 1950s originated from infected nursery stock imported from Europe (Gould et al. 1955; Gould 1966; Savile 1955, 1973). On the contrary, the present study shows that these outbreaks were likely caused by *C. reticulata* that spread to nurseries from native *Ledum* spp.: (*i*) samples of both *Ledum* and cultivated rhododendrons from Long Beach, Washington, one of the first sites of these outbreaks, are preserved in PUR; (*ii*) the urediniospores are smaller than typical for *C. rhododendri*; (*iii*) the warm coastal habitat of Washington would be unusual

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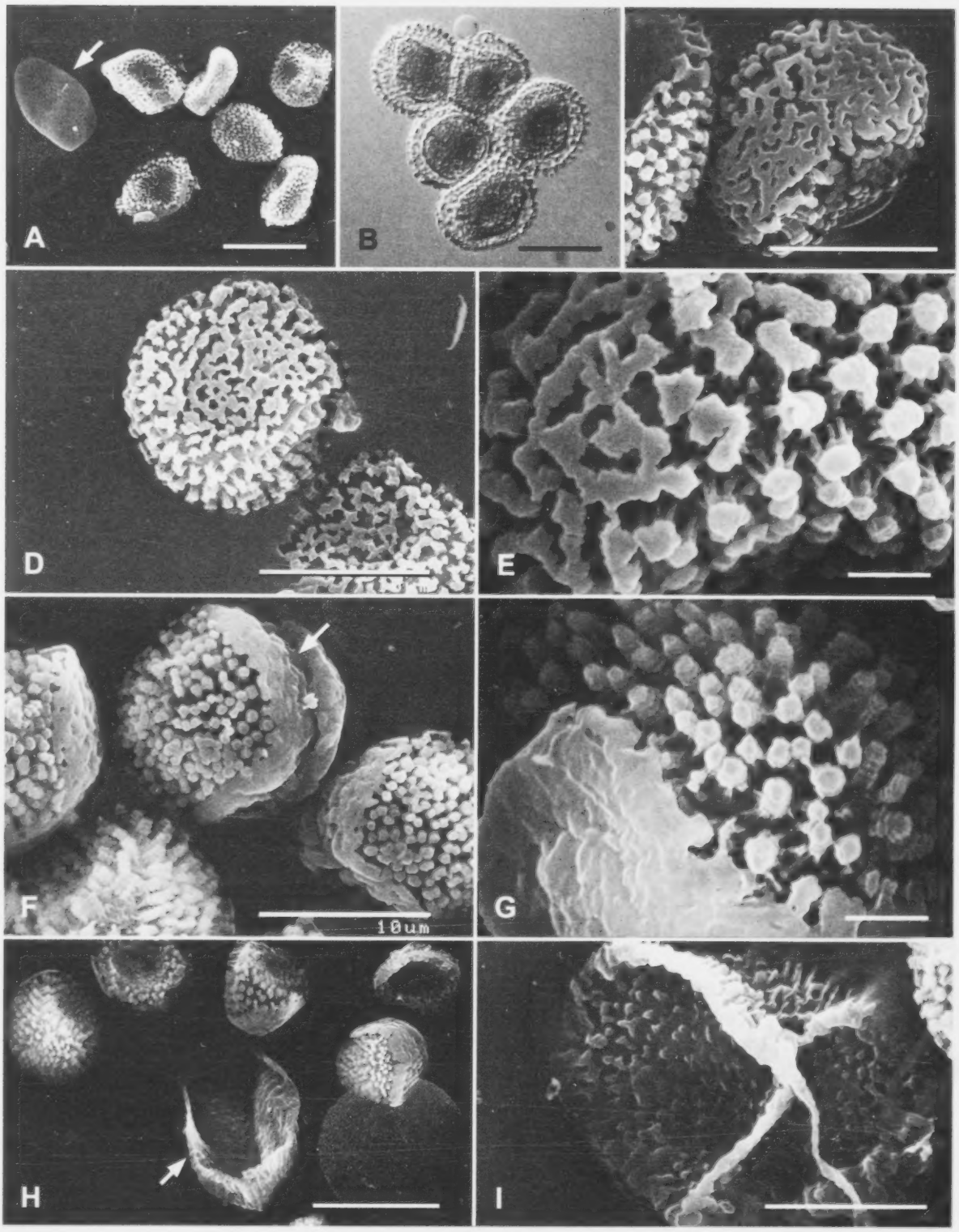

for *C. rhododendri*, which is native to far northern and alpine habitats in North America and Europe; *Chrysomyxa reticulata* appears to have a much more widespread habitat distribution; (*iv*) the morphology and spore size is identical for the rusts on both host genera (Figs. 2, 7C, and 7D).

It should be noted that not all rusts found on cultivated

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rhododendrons in North America are *C. reticulata*. *Chrysomyxa nagodhii* was also identified on one specimen from Vancouver Island; another plant, with a notation that it was imported from Tibet, appeared to be *C. rhododendri*. SEM has elucidated the unique morphology of the spores of *C. reticulata*, and rusts appearing on cultivated rhododendrons should be identified by microscopic examination. Planting rhododendrons near native *Ledum* spp. should be discouraged.

On cultivated rhododendrons, *C. reticulata* does not appear to produce telia; on *Ledum*, telia were found only on the type material, the above-mentioned Wisconsin sample, and possibly one from northern British Columbia (DAVFP 20261). At the type locality in Kananaskis, Alberta, this rust was producing uredinia earlier than either *C. ledicola* or *C. nagodhii*, which were present in the same area. Gelatinous sori among the uredinia developed into telia when the infected leaves were placed in a moist chamber for several days. When mature, these telia were used to infect spruce, thus elucidating the entire life cycle. Naturally infected spruce were not found, however, in the Kananaskis location later in the growing season. Perhaps this rust rarely produces telia in nature. I considered the possibility that the telia used for inoculation were actually of *C. nagodhii*. The aecial state produced on spruce needles, however, differed in several ways from *C. nagodhii*: a delicate, ephemeral peridium without coarse striate side walls, pale rather than deep orange spores, smaller aeciospores (Fig. 2) with a smooth longitudinal cap having a central groove (Fig. 7F, arrow), and narrower intercellular hyphae (3–4 µm compared with 5–6 µm in *C. nagodhii*).

It is possible that *C. reticulata* has been introduced to other areas of the world by the importation of rhododendrons from the U.S.A. Bennell (1985) noted that a rust introduced to Scotland on planting stock from the western U.S.A. in 1980 infected rhododendron species that were resistant to the *C. rhododendri* rust already present; other species that were normally highly susceptible did not become infected. The rust was assumed to be a new pathotype of *C. rhododendri*. It is also possible that the introduced rust was *C. reticulata*.

Chrysomyxa rhododendri de Bary, Bot. Z. 37: 809. 1879. Figs. 8A–8H

≡*Chrysomyxa ledi* var. *rhododendri* (de Bary) Savile, Can. J. Bot. 33: 491. 1955.

=*Uredo rhododendri* DC., Flore Fr. 6: 86. 1815.

≡*Chrysomyxa ledi* var. *rhododendri* (DC.) Savile, Can. J. Res., C, 28: 325. 1950. [nom.nud.]

≡*Coleosporium rhododendri* (DC.) J. Schröt. (subgen. *Melampsoropsis*), in Cohn, Beitr. Biol. Pflanzen, Band I, Heft 3, Pt. II, p. 56. 1879. [Based on uredinia].

=*Caeoma rhododendri* Link, Spec. Plant. II, p. 16. 1825.

=*Caeoma piceatum* Link, in Linné, Spec. Plant. VI, 2: 62, 1825. p.p.

=*Melampsora rhododendri* Thüm., 1880. [*fide* Hiratsuka et al. 1992].

=*Melampsoropsis rhododendri* Arthur, Résult. Sci. Congr. Bot. Vienne, 1905, p. 338. 1906.

=*Aecidium abietinum* Alb. & Schwein., Consp. Fung., p. 120. 1805. p.p. [combined aecia of *C. ledi* and *C. rhododendri* (Sydow and Sydow 1915)].

=*Erysibe rhododendri* Wallr., Flora Cryptogam. Ger. II, No. 1622, p. 199. 1833. [Based on uredinia].

LECTOTYPE: On *Rhododendron hirsutum* L., Schächenthal in Uri, Switzerland, de Bary (syntype K!).

HOSTS AND DISTRIBUTION: *Chrysomyxa rhododendri* has a holarctic distribution, occurring in Europe, Greenland, far northern North America, Siberia, China, Korea, Taiwan, and Tibetan East Himalayas. The aecial stage is found on *P. abies*, *P. sitchensis* (Japan, Britain, Europe, not in North America); *P. jezoensis*, *P. glehnii* (Japan); *Picea brachytyla* (Franchet) Pritzel (China), and *P. obovata* (eastern Siberia). Numerous species of rhododendron, both wild and cultivated, have been documented as hosts to *C. rhododendri*. Some of these reports may not be accurate because of confusion with other species. For example, many reports of *C. rhododendri* on cultivated rhododendrons in North America are probably *C. reticulata* or *C. nagodhii* (see Notes under *C. reticulata*). Therefore mention will be made of only native hosts in Europe (*Rhododendron ferrugineum* L., *R. hirsutum*, and their hybrids) and North America and Greenland (*Rhododendron lapponicum* (L.) Wahlenb.). For hosts affected in Asia and in cultivation in Europe and North America, the reader is referred to lists elsewhere (Gäumann 1959; Leppik 1974; Bennell 1985; Farr et al. 1996). Importation of horticultural varieties of rhododendrons has resulted in spread of this rust to New Zealand and Australia (Bennell 1985).

Description

On *Rhododendron*. Uredinia and telia hypophyllous on leaves of previous year; uredinia also on leaf petioles, fruit pedicels, and twigs. Uredinia scattered, partially or completely covering underside of some leaves but absent from others, erumpent through epidermis, round, pulvinate, 0.2–0.7 mm wide, larger on twigs, flat-bottomed in cross section, with an inconspicuous peridium of collapsed, thin-walled cells. Urediniospores mostly ellipsoidal or ovoid, occasionally subglobose or globose, one or both ends slightly flattened or with a small cap, part of a shallow longitudinal stripe containing shallow, irregular bumps, 18–32(–36) × 14–22 µm ($\bar{x}$ = 23.6 ± 3.0 × 17.7 ± 2.0 µm), apricot color (5B6); wall hyaline, <1 µm thick; wall plus warts 1.2–2.9 µm thick. Telia in groups, confluent, erumpent through epidermis, larger and more irregular in shape than uredinia, up to 1 mm long. Teliospores cuboid to ellipsoidal or irregular, 20–28(–34) × 12–21 µm, wall colorless, thin, smooth. Basidiospores globose to subglobose, 8–10 × 8 µm, with a small apiculus.

On *Picea*. Spermogonia and aecia on yellowed zones of current-year needles, causing premature defoliation. Spermogonia prominent, round or elongated on needle surface, amphigenous; in cross section, hymenium broad and flat to shallowly concave, 140–220 µm wide × 110–150 µm high. Spermatia globose to subglobose, 2.5–3.7 × 2.0–3.3 µm. Aecia amphigenous, variable in size, 0.3–1.3 mm wide, single or confluent. Aeciospores variable in shape from globose to ellipsoidal or ovoid, with one or both ends flat or with a

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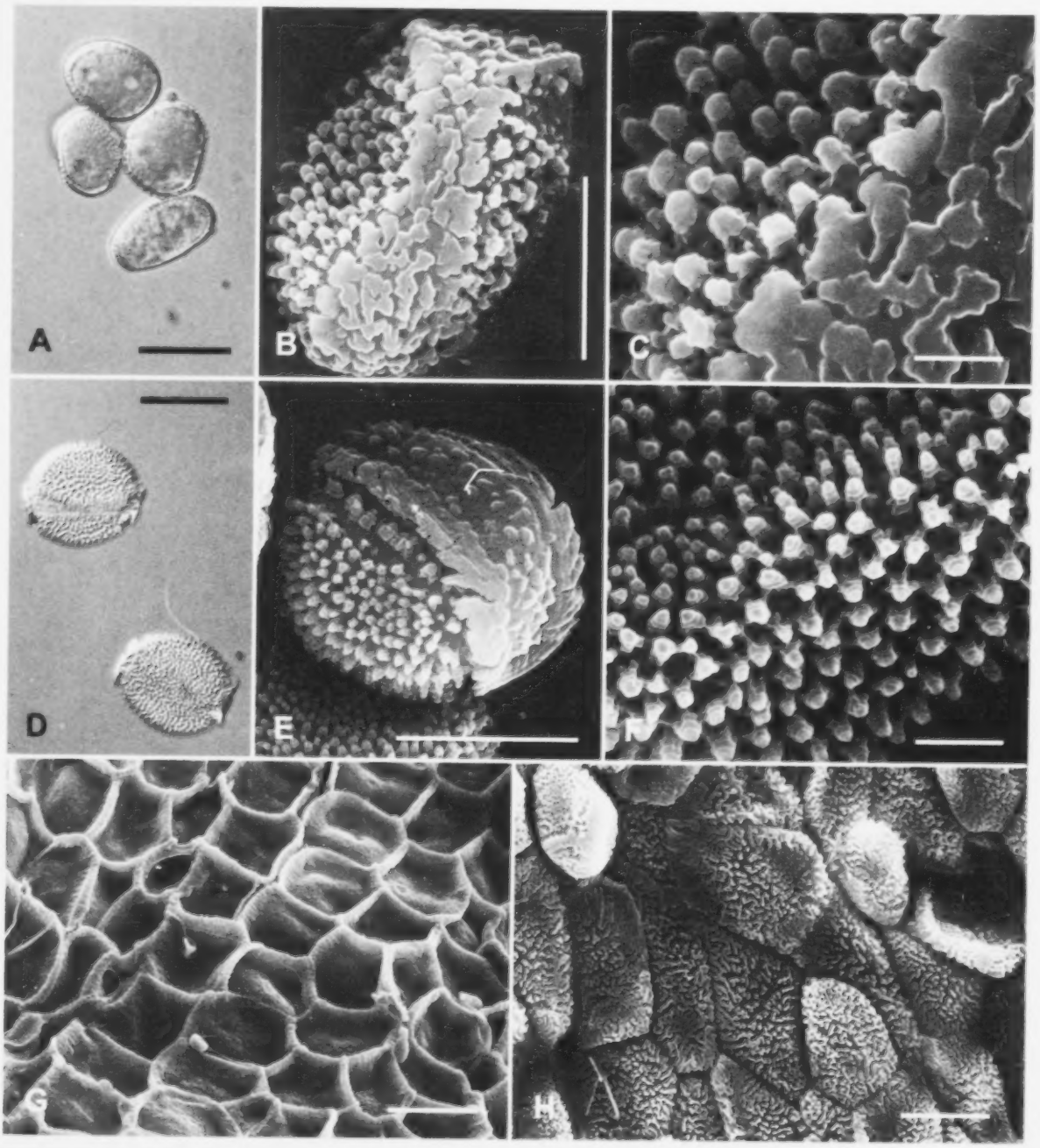
Fig. 8. *Chrysomyxa rhododendri*. (A–C) Urediniospores from *Rhododendron lapponicum*, Manitoba (PUR 53201): (A) by LM; (B) single spore by SEM, showing longitudinal stripe with shallow, irregular bumps; and (C) details of surface ornamentation. (D–F) Aeciospores from *Picea abies*, Switzerland (CFB 22181): (D) by LM, showing small caps at ends; (E) by SEM, showing longitudinal smoother area with irregular bumps; and (F) details of surface ornamenation. (G, H) Aecial peridium: (G) shallowly concave, smooth outer surface of cells; (H) inner cell surface, showing labyrinthine appearance of warts. In Figs. 8A, 8D, 8G, and 8H, scale bars = 20 μm; in Figs. 8B and 8E, scale bars = 10 μm; in Figs. 8C and 8F, scale bars = 2 μm.



small delicate cap, part of an indistinct longitudinal stripe containing irregular shallow bumps, 18–30 × 16–22 μm ($\bar{x}$ = 23.6 ± 2.7 × 18.6 ± 1.5 μm), light orange (5B5 or 5A5); wall hyaline, wall plus warts 2.0–3.3 μm thick. Peridium delicate, shredding at maturity, but persistent; on outside, cells shallowly concave, smooth; on inside, convex with shallow warts, sometimes appearing labyrinthine; lateral walls narrow (~2 μm), striate.

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Notes

Unlike the *Ledum* rusts, which are different morphologically between Europe and North America, *C. rhododendri* on native rhododendrons in Europe and northern Canada is remarkably similar. The urediniospores are fairly uniform in both spore size and surface morphology. Whereas telia are abundant on European native rhododendrons, however, they have not been reported in North America on *R. lapponicum*, and therefore the rust is unknown on spruce on this continent. Whether this suggests a different race or species of the rust (Savile 1950), or merely a response to a different host or climate, is unknown. In Britain, where *C. rhododendri* is an introduced species, the stage that develops also varies with the host, with uredinia most common. On *R. ponticum*, though, telia predominate (Wilson and Henderson 1966). Inoculation experiments suggest that the host strongly influences the stage that develops. When cultivated rhododendrons were inoculated with the same inoculum under uniform conditions, uredinia only, telia only, or both uredinia and telia were produced, depending on the host (Bennell 1985).

The connection of the aecial and telial stages of *C. rhododendri* was proven by de Bary (1879) and confirmed by Klebahn (1905). In subalpine regions of Europe, teliospores appear on native rhododendrons in early summer during flowering of the host. Basidiospores infect young spruce needles, producing spermogonia within 10 d, and later aecia, from late July until early September. Aeciospores infect mature rhododendron leaves and form uredinia. The next spring, telia develop from overwintering mycelium (Gäumann 1959). On cultivated rhododendrons, however, the behavior of *C. rhododendri* may vary considerably, depending on host phenology, prevailing climate, and probably the pathotype of the rust involved. Thus in Britain, five major life-cycle patterns have been recognized: a single annual cycle of urediniospores, recycling of uredinia in the growing season, year-round sporulation in sheltered conditions, alternation to spruce along with any of the previous patterns, and obligatory alternation (Bennell 1985).

de Bary (1879) clearly illustrated the major differences between the peridial cells of *C. ledi* and *C. rhododendri* and this study confirms his observations. The wide (3–6 µm or more) coarse striate margins of the peridial cells of *C. ledi* are much more obvious than the more delicate lateral margins (2 µm) of *C. rhododendri*. The mean urediniospore size of the two species is very similar, but the aeciospores of *C. ledi* tend to be longer than those of *C. rhododendri* (Figs. 2A and 2B). Whereas *C. ledi* spores have a narrow groove and long tapered warts, *C. rhododendri* has an indistinct smooth or irregular longitudinal stripe and cylindrical warts. The habitat differences (*C. rhododendri* occurs mainly in subalpine regions in Europe, *C. ledi* at lower elevations farther north) also support the separation of these two taxa as distinct species. *Chrysomyxa roanensis* (Arthur) Arthur and *Chrysomyxa piperiana* Sacc. & Trotter ex Cummins, two other rhododendron rusts endemic to North America, both have longer spores than *C. rhododendri* (Savile 1950; Crane 2000).

A specimen from China was consistent with the species description presented here. The samples from Japan, however, had a different surface ornamentation, with warts very crowded and often joined laterally at the top. They may be a distinct species; therefore these samples were not used in compiling the description.

During rainy summers, *C. rhododendri* may cause serious damage to *P. abies* in Europe (Biraghi 1966; Böhmer et al. 1998). Severe infection may occur also in Britain on *P. abies* (Gardener's Chronicle 1943), whereas *P. sitchensis* appears to be more resistant (Wilson and Henderson 1966). Recent studies (Bauer et al. 2000) in Austria show that afforestation and regeneration of Norway spruce is seriously impaired in regions of frequent attack by *C. rhododendri*. The fungus reduces photosynthetic capacity of heavily infected trees, reducing carbohydrate production, and significantly decreasing radial growth (Oberhuber et al. 1999).

Chrysomyxa rhododendri is the most widely distributed rust of rhododendrons in cultivation (Bennell 1985). It disfigures and discolors ornamental rhododendrons, reducing their value. In cultivation, the rust attacks over 50 new host species not known to be affected in their wild habitats. Hybrids between susceptible and nonhost species are often susceptible (Bennell 1985). Although *C. rhododendri* probably exists in North America on cultivated rhododendrons, transfer of native rusts (*C. nagodhii*, *C. reticulata*, *C. ledicola*) to these hosts also occurs. The identity of rhododendron rusts on this continent should be verified by careful microscopic examination.

Chrysomyxa vaccinii (Ziller) P.E. Crane, comb.nov. Figs. 9A–9C

≡*Chrysomyxa ledi* var. *vaccinii* Ziller, in Savile, Can. J. Bot. 33: 492. 1955. [basionym].

TYPE: On *Vaccinium parvifolium* Smith, Qualicum Beach, British Columbia, 17 Jun 1955, W.G.Z. (Holotype DAOM 46500, Isotypes DAVFP 9450! PUR 54765!).

HOSTS AND DISTRIBUTION: Telia and uredinia of *C. vaccinii* are known only on *Vaccinium parvifolium* Smith from Vancouver Island, Queen Charlotte Islands, and coastal British Columbia (Ziller 1974). Aecia are unknown, but likely occur on *P. sitchensis*, since telia occur regularly, and the rust has been collected near this spruce species.

Description

On *Vaccinium parvifolium*. Uredinia and telia hypophyllous on overwintered leaves of previous year, on discolored patches between major veins. Uredinia in the same or different patches from telia, round to slightly elongated, 0.2–0.3 mm wide, subepidermal. Urediniospores variable in size and shape, mostly ellipsoidal, ovoid, or oblong, often with one or both ends flat, (16)20–32 × 11–20 µm ($\bar{x}$ = 25.1 ± 3.1 × 16.1 ± 2.0 µm); wall hyaline, 0.3–0.6 µm thick; wall plus warts 1.6–2.5 µm thick; warts flat-topped, irregular in size and shape, annulate, stellate in surface view because of basal connections, sometimes joined into ridges. Telia in groups, single or confluent, sometimes in elongated ridges, subepidermal with flat hymenium, 0.2–0.7 mm wide, erumpent through epidermis. Teliospores catenulate, cuboid to oblong, 9–22 × 7–12 µm. Spermogonia and aecia unknown.

Notes

When Savile (1955) reduced several species of *Chrysomyxa* to varieties of *C. ledi*, he included Ziller's newly found

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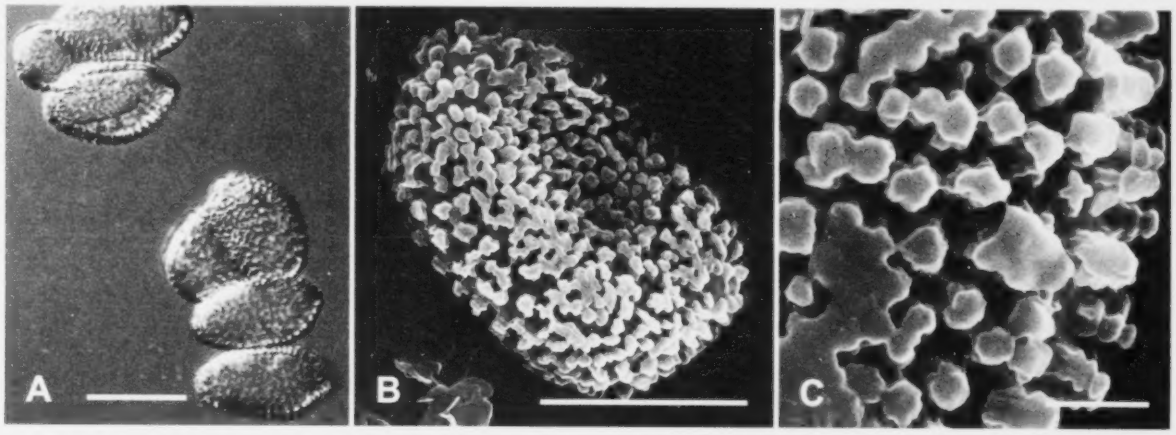
Fig. 9. *Chrysomyxa vaccinii* on *Vaccinium parvifolium* (Q.C.I., B.C., PUR 54528). (A–C) Elongated urediniospores: (A) by LM; (B) single spore by SEM; and (C) irregular surface ornamentation. In Fig. 9A, scale bar = 20 µm; in Fig. 9B, scale bar = 10 µm; in Fig. 9C, scale bar = 2 µm.



rust on *Vaccinium*, mainly because of spore size. However, one of the main reasons for establishing these varieties was the difficulty of identifying the aecial states on spruce. Because the aecial stage of *C. vaccinii* is so far unknown, inclusion of this species as a variety of *C. ledi* seems unjustified. It should be noted also that *C. vaccinii* has been reported to be most similar to *C. chiogenis* (Ziller 1974), which was not included in the *C. ledi* complex. SEM studies, along with hosts in subfamily Vaccinioideae, support the close relationship of these species (see Notes under *C. chiogenis*).

Chrysomyxa vaccinii is the only North American species in the genus that occurs on *Vaccinium*, perhaps because many species in this host genus have deciduous leaves and this would not permit overwintering of the mycelium. *Chrysomyxa taihaensis* Hirats. f. & Hashioka occurs on *Vaccinium merrillianum* Hayata in Japan, but uredinia have not been reported for that species, and the teliospores are considerably larger (27–45 × 12–24 µm) than those of *C. vaccinii* (Hiratsuka and Hashioka 1935).

Inoculation of *Picea* and *Tsuga*, the two conifers found near the telial host (Savile 1955), with *C. vaccinii* basidiospores is needed to confirm the complete life cycle of this rust.

Peridermium zilleri P.E. Crane, anam.nov., a new *Peridermium* on *Picea sitchensis* Figs. 10A–10E

TYPE: On *Picea sitchensis*, Yakoun L., Graham Is., Q.C.I., British Columbia, 12 Sept. 1988, D. Redfern (Holotype DAVFP 23796; Isotype DAOM 198870).

ETYMOLOGY: Named in honor of W.G. Ziller, an authority on tree rusts and former curator of the Mycological Herbarium, Pacific Forestry Centre, Canadian Forest Service, Victoria, B.C.

HOSTS AND DISTRIBUTION: *Peridermium zilleri* is known on *P. sitchensis* from the Queen Charlotte Islands, coastal British Columbia, and from the southwest coast of Vancouver Island. Although a specimen from Vancouver Island had shorter spores than the samples from the Queen Charlotte Islands, the morphology was very similar and therefore it is included here.

Description

In *Picea sitchensis*. Spermogonia ignota. Aecia in lineis chloroticis acuum arborearum huius anni, in ordinibus duobus in superficie supera, discreta, angusta, similia tubis, 0.5–1.3 mm lata. Aeciosporae fusiformae, 23–39(–44) × 10–19 µm ($\bar{x}$ = 29.7 ± 4.3 × 14.2 ± 1.6 µm), truncatae vel in extremis acutae; pars sporae velata a superficie lata et longitudinale et leviore de summis verrucis dorsa formantibus; alibi verrucae cylindricae et annulatae, bases grallae-formes; summae latae et irregulares aspectu, 1.6 µm altae; tunica indistincta, 0.8 µm vel magis tenuis. Peridium persistens, cum cellulis in apice brunneis, dehiscens in lateribus; cellulae elongatae, superficies externa levis, paulo concava; superficies interna paulo convexa, cum verrucis longis et angustis et frequenter congregatis, nonnumquam speciem labyrinthi formantibus.

On *Picea sitchensis*. Spermogonia unknown. Aecia on chlorotic bands of current-year needles, in two rows on upper surface, discrete, narrow, tube-like, 0.5–1.3 mm wide. Aeciospores fusiform, 23–39(–44) × 10–19 µm ($\bar{x}$ = 29.7 ± 4.3 × 14.2 ± 1.6 µm), truncate or pointed at ends; part of spore covered with a broad longitudinal smoother area consisting of wart tops joined into ridges; warts elsewhere cylindrical and annulate, 1.6 µm high, with stilt-like bases, tops broad and irregular in surface view; wall indistinct, 0.8 µm or less thick. Peridium persistent, with brownish cells at apex, dehiscent at sides; cells elongated, outer surface smooth, shallowly concave; inner surface slightly convex, with long, narrow, crowded warts, sometimes joined into a maze-like pattern.

Notes

The similar aeciospore morphology of *Peridermium zilleri* to species in the genus *Chrysomyxa* suggests that it belongs in that genus. However, without spermogonia, this anamorph cannot be placed with certainty in *Chrysomyxa* and may also belong in *Pucciniastrum*. Two species of *Chrysomyxa* also lack spermogonia: *C. chiogenis* and a west coast variety of *C. ledicola* (Crane 2000). Although *P. zilleri* resembles *C. chiogenis* in morphology, the only reported host of *C. chiogenis*, *Gaultheria hispidula*, does not occur on either of the islands where this *Peridermium* is found (Pojar and

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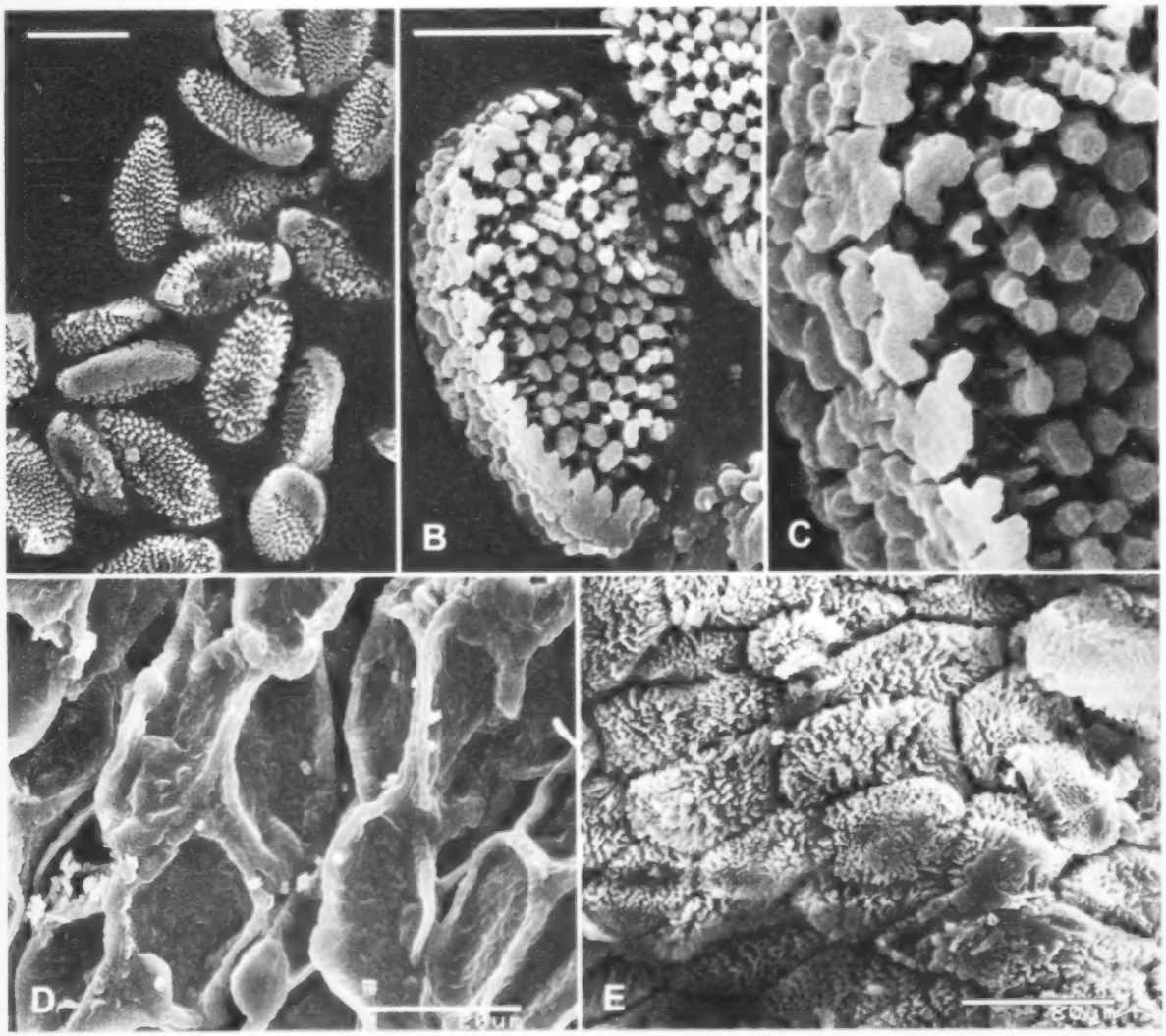
Fig. 10. *Peridermium zilleri* on *Picea sitchensis*. (A–C) Aeciospores: (A) group of elongated spores; (B) single spore with smoother cap over part of spore; (C) details of cap and annulate warts with broad tops. (D, E) Aecial peridium: (D) outer surface; (E) densely warted inner surface. In Figs. 10A, 10D, and 10E, scale bars = 20 μm; in Fig. 10B, scale bar = 10 μm; in Fig. 10C, scale bar = 2 μm.



Mackinnon 1994; Clark 1998; Douglas et al. 1999). Aeciospores of *Peridermium zilleri* differ from those of *C. chiogenis* in their longer, narrower shape; more obvious cap-like ends; and less-developed basal connections between warts. Both have a broad longitudinal smoother area on the aeciospores, but in *Peridermium zilleri* it is not continuous, but broken into ridges (Figs. 10A–10C). The inner surface of the peridial cells of *C. chiogenis* is shallowly and sparsely ornamented, whereas in *Peridermium zilleri* the warts are long, narrow, and densely crowded. Spore morphology and size are also different from the other west coast species with elongated spores, *C. piperiana* (Ziller 1974; Crane 2000). For the above reasons, it seems desirable to recognize this rust as a distinct species.

Based on distribution and spore morphology, the most likely telial state of *Peridermium zilleri* is *C. vaccinii*, for which inoculation experiments have not been done to determine the aecial state.

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Appendix

Specimens examined

C. cassandrae

On *Chamaedaphne calyculata*. CANADA: Alberta: Goose Mtn. Fire Tower Rd., 10 km NW of Swan Hills, 28 June 1981, J.D. Johnson (CAFB 811457); 13.3 km N of Calling L., Hwy. 813, 13 June 1997, Y.H. et al. (CFB 22069, 22156). British Columbia: Fort Nelson, 20 July 1966, D.G. Lund & J. Grant (DAVFP 17131). Manitoba: Berens River, 29 July 1933, G.R. Bisby (PUR 44378). Northwest Territories: Indin L., District of Mackenzie, 64°17′N, 115°12′W, 12 Aug 1949, W.J. Cody & B.J. McCanse (PUR 52049). Nova Scotia: Pictou, 13 June 1910, W.P. Fraser (PUR 4847). Yukon Territory: 0.75 mi (1 mi = 1.609 km) NE of Mayo, 2 Aug. 1949, J.A. Calder et al. (PUR 52026). FINLAND: Karelia, 18 Aug. 1899, J.I. Lindroth (PUR 511). RUSSIA: Shisuka, S. Saghalien [Sakhalin], 12 Aug. 1928, N. Hiratsuka (PUR F12673); Aihama, S. Saghalien, 17 July 1927, N. Hiratsuka (PUR F12674). U.S.A.: Wisconsin: Hope L. bog nr. Cambridge, Jefferson Co., 12 June. 1965, H.C. Greene (PUR 61510).

On *Picea glauca*. CANADA: Alberta: Edmonton, 19 July 1997, P.E.C. (CFB 22128, from inoculation). On *P. mariana*. CANADA: Alberta: 13.3 km N of Calling L., Hwy. 813, 13 June 1997, P.E.C. et al. (CFB 22118, 22132). Nova Scotia: Pictou, 24 July 1910, W.P. Fraser (PUR 4809). U.S.A.: Maine: Kittery Pt., July [no year], R. Thaxter (PUR 4798). New York: Junius Swamp, July 1905, E.J. Durand (PUR 4800). On *P. pungens*. CANADA: Alberta: Edmonton, 19 July 1997, P.E.C. (CFB 22126, from inoculation). U.S.A.: Wisconsin: July 1941, E.L. Chambers (PUR 49816). On *P. rubens*. CANADA: Ontario: Sparrow L., 26 Aug. 1907, J.C. Arthur (PUR 4820). Nova Scotia: Pictou, 24 July 1910, W.P. Fraser (PUR 4824, from inoculation).

C. chiogenis

On *Gaultheria hispidula*. CANADA: British Columbia: Prince George, 4 Sept. 1950, W.G.Z. (DAVFP 6047); Wells, 20 July 1954, J. Grant & C.B. Cottrell (DAVFP 9388); Prince George, 28 June 1966, J. Grant (DAVFP 17135). Quebec: Mi 13, Clova, 24 June 1931, C.G. Riley (WINF(M) 1793). U.S.A.: Wisconsin: Forest Co., June 1893, J.J. Davis (PUR 4899, Type).

On *Picea glauca* (from inoculation). CANADA: Ontario: Bear Is., L. Timagami, 1928, G.D. Darker (BPI 0190499), 7 Aug. 1924 (BPI 190501); 12 Sept. 1924, W.R. Watson (BPI 190502, 190503).

C. ledi

On *Ledum palustre*. FINLAND: West of Kemijärvi, 7 Aug. 1998, P.E.C. (CFB 22203); Kaihuavaara, 7 Aug. 1998, P.E.C.

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(CFB 22205). GERMANY: Pommena. Wald vor Stolpmünde, May 1889, P. Sydow (PUR F23); Berlin, Grunewald, 29 June 1895, P. Magnus (PUR 577, Type locality). RUSSIA: Shisuka, S. Saghalien [Sakhalin], 12 Aug. 1928, N. Hiratsuka (PUR 12687). SWEDEN: Talum, E Museo Botanico Upsaliensi, 6 July 1900, O. Juel (DAVFP 19570). On *L. palustre* ssp. *diversipilosum* Hara. JAPAN: Horomui, Ishikari [Hokkaido], 14 June 1925, N. Hiratsuka (PUR F512); 10 Sept. 1923 (PUR F12684); Mt. Nupukaushi, Tokachi [Hokkaido], 6 June 1925, N. Hiratsuka (PUR F12685); Mt. Kuro-dake, Ishikari [Hokkaido], 5 Aug. 1925, N. Hiratsuka (CFB F12686).

On *Picea abies*. FINLAND: Vikingarri, 12 Aug. 1995, Y.H. (CFB 22017, 22019); Kittia, 13 Aug. 1995, Y.H. & R. Jalkanen (CFB 22061); Ruka, Kuusamo, 20 Sept. 1983, R. Jalkanen (CFB 22159); Sierita, Rovaniemi, 24 Aug. 1981, R. Jalkanen (CFB 22160); Siperia, Rovaniemi, 15 Sept. 1997, R. Jalkanen (CFB 22161) and 28 Aug. 1998 (CFB 22178); west of Kemijärvi, 7 Aug. 1998, P.E.C. (CFB 22204); Mustiala, July 1879, P.A. Karsten (PUR 517, as *Peridermium coruscans*). RUSSIA: Levashovo nr. Petersburg, Aug. 1882, W. Tranzschel (PUR F316). SWEDEN: "Dalaro" nr. Stockholm, Aug. 1899, G. v. Lagerheim (PUR F514). On *P. glauca*. FINLAND: Siperia, Rovaniemi, 28 Aug. 1998, R. Jalkanen (CFB 22177). On *P. mariana*. FINLAND: Siperia, Rovaniemi, 28 Aug. 1998, R. Jalkanen (CFB 22179).

C. nagodhii

On *Ledum decumbens*. CANADA: British Columbia: Mi 402, Alaska Hwy., Summit L., 15 June 1972, C.S. Wood (CFB 22095, ex DAVFP 20264). On *L. groenlandicum*. CANADA: Alberta: 3 mi W, 0.5 mi S of Harman Valley, 56°06′N, 116°55′W, 15 June 1965, C.R. Layton (CFB 6672); 2 mi W of Miette Hot Springs, Jasper Natl. Park, 53°07′N, 117°48′W, 5 Aug. 1966, P.J. Maruyama & Y.H. (CFB 7516); Sir Winston Churchill Prov. Park, Lac la Biche, 19 June 1996, P.E.C. (CFB 22023); Hargwen Rd., E of Obed Summit, Hwy. 16, 26 June 1996, Y.H. et al. (CFB 22035); Beaver Hills L. Tr., Jasper Natl. Park, 6 Sept. 1996, P.E.C. (CFB 22064); Pine Ridge Nursery, Smoky Lake, 26 Sept. 1996, P.E.C. (CFB 22066); Red Earth Cr., Banff Natl. Park, 10 July 1998, P.E.C. (CFB 22189). British Columbia: Prince George, 16 Sept. 1955, W.G.Z. (DAVFP 9745); Field, 30 June 1958, W.G.Z. (DAVFP 10850); South Westminster, 22 June 1922, J.S. Boyce (PUR 4794). Newfoundland: St. Anthony, 21 July 1951, D.B.O.S. & J. Vaillancourt (PUR 54531, DAOM 45442). Northwest Territories: 60 mi S of Wrigley, 62°20′N, 123°30′W, 15 July 1965, E. Gautreau (CFB 6698); Ft. Liard Tower, 13 July 1966, E. Gautreau & Y.H. (CFB 7625). Nova Scotia: Pictou, 15 June 1910, W.P. Fraser (PUR 4875). Quebec: Great Whale R., 12 July 1949, D.B.O.S. (PUR 52013, ex DAOM 23505). U.S.A.: Alaska: Chicken, 15 July 1959, W.G.Z. (DAVFP 11556); Pitchfork Falls, Skagway, July 1930, H.E. Parks (PUR 44375). Wisconsin: Sturgeon Bay, 24 June 1913, J.J. Davis (PUR 4874). On *Ledum* sp. CANADA: Manitoba: Chisel L., 18 Aug. 1970, R.C. Tidsbury (CFB 20195). Saskatchewan: Pasquia Hills, 28 July 1970, R.C. Tidsbury (CFB 20163). On *Rhododendron* sp.: CANADA: British Columbia: Whalley, 3 Sept. 1958, E. Fridell & C. Gibson (DAVFP 10779, as *C. ledi* var. *rhododendri*).

On *Picea glauca*. CANADA: Alberta: Pine Ridge Nursery, Smoky Lake, 14 Aug. 1996, P.E.C. (CFB 22053). British Columbia: Prince George, 2 Aug. 1954, J.A. Calder et al. (DAOM 45454). On *P. mariana*. CANADA: Alberta: Edmonton, 28 July 1997 & 4 Aug. 1997, P.E.C. (CFB 22133, from inoculation); Edmonton, 25 July 1997, P.E.C. (CFB 22134, from inoculation). British Columbia: Prince George, 4 Sept. 1950, W.G.Z. (DAVFP 6055). On *P. pungens*. CANADA: Alberta: St. Albert, 13 Aug. 1997, P.J. Maruyama (CFB 22155); Edmonton, 11 Sept. 1996, P.E.C. (CFB 22058); Edmonton, 28 May 1998, P.E.C. (CFB 22186, from inoculation). On *P. rubens*. CANADA: Nova Scotia: Pictou, 31 July 1909, W.P. Fraser (PUR 4852, from inoculation); Pictou, 24 July 1910, W.P. Fraser (PUR 4854, from inoculation).

C. neoglandulosi

On *Ledum glandulosum*. CANADA: Alberta: Lower Cascade Fire Rd., Banff Natl. Park, 9 June 1977, P. Achuff (CAFB 810491); 7 mi W of Waterton Lakes Natl. Park, 19 Aug. 1966, N.W. Wilkinson (CFB 7464); 2.5 km along Akamina Pass Trail, Waterton Lakes Natl. Park, 6 July 1997, P.E.C. (CFB 22174, Isotype; CFB 22079). British Columbia: Arthur L., Falkland, 21 July 1952, W.G.Z. (DAVFP 8117); Falkland, 25 July 1952, W.G.Z. (DAVFP 8138); Kelowna, 13 Aug. 1954, L.M. Wallington & B.A. Sugden (DAVFP 9427); Penticton, 17 Aug. 1971, W.G.Z. (DAVFP 19993); Monashee Pass, 5 July 1953, J.A. Calder & D.B.O.S. (PUR 54527, ex DAOM 45484). U.S.A.: Idaho: Josephus Lakes, Custer Co., 5 Aug. 1916, J.F. Macbride & E.B. Payson (PUR 4857). Montana: Sylvan Geysers, Yellowstone Natl. Park, 26 July 1899, J.B. Ellis (PUR 4856); Alpine, 5 Aug. 1921, E. Bartholomew (PUR 4858). Nevada: Jarbidge, 7 July 1912, Nelson & Macbride (PUR 4859). On *L. glandulosum* × *L. groenlandicum*. CANADA: Alberta: Red Earth Cr., 7 mi from highway, Banff Natl. Park, 7 July 1959, R.T. Ogilvie (CAFB); Red Earth Fire Rd., mile 33, Banff Natl. Park, 16 June 1965, V.B. Patterson (CFB 7399).

On *Picea engelmannii*. CANADA: Alberta: Trail to Akamina L., nr. Cameron L., Waterton Lakes Natl. Park, 10 Aug. 1998, P.E.C. (CFB 22184). British Columbia: Kelowna, 13 Aug. 1954, L.M. Wallington & B.A. Sugden (DAVFP 9390); 1 mi E of Park Headquarters, Manning Prov. Park, 10 Aug. 1953, J.A. Calder & D.B.O.S. (PUR 59392). U.S.A.: Idaho: Scolfield Cr., Clearwater Co., 20 July 1965, J.W. Kimmey (PUR 61362).

C. reticulata

On *Ledum decumbens*. CANADA: Alberta: Unnamed L., 5 July 1966, J. Susut & J. Petty (CFB 7334). British Columbia: Muncho L., 9 June 1972, C.S. Wood (DAVFP 20261). On *L. groenlandicum*. CANADA: Alberta: Tunnel Trail, S of Ribbon Cr. Trail, Kananaskis, 1 June 1998, P.E.C. (CFB 22183, Type); Kananaskis For. Exp. Stn., Ribbon Cr., 6000 ft, 9 Oct. 1958, R.T. Ogilvie (CAFB). British Columbia: Daisy Lake, 13 Oct. 1924, J.S. Boyce (PUR 4881); Ft. St. John, 29 June 1965, R.O. Wood (DAVFP 16754). Nova Scotia: Pictou, 26 June 1909, W.P. Fraser (PUR 4866); Numa Cr. Trail, Kootenay Natl. Park, 28

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July 1965, V.B. Patterson (CFB 6809). U.S.A.: Wisconsin: Three Lakes, Jul 1893, J.J. Davis (PUR 4877). On *Rhododendron odoratum*. U.S.A.: Washington: Long Beach, 4 Apr. 1954, C.J. Gould (PUR 53445). On *Rhododendron racemosum* ×*ciliatum*. CANADA: British Columbia: Saanich, Vancouver Is., 18 July 1958, W.G.Z. et al. (DAVFP 10764); 17 July 1958, W.G.Z. & G.S. Brown (DAVFP 10762). On *Rhododendron* sp. CANADA: British Columbia: Vancouver, 27 Nov. 1998, Y.H. (CFB). U.S.A.: California: Oct. 1962 (PUR 57912, 57913). Washington: Long Beach, 3 Aug. 1955, Wheeler et al. (PUR 54533).

On *Picea glauca*. CANADA: Alberta: Edmonton, 9 July 1998, P.E.C. (CFB 22182, from inoculation).

C. rhododendri

On *Rhododendron ferrugineum*. SWITZERLAND: Trail to Nair L., St. Moritz, Engadine, 18 Aug. 1998, R. Berndt (CFB 22180); Canton of Valais, 20 Aug. 1954, E. Mayor (DAVFP 11964). ITALY: Tirol, Brixen [Bressanone], 29 July 1891, P. Dietel (PUR 530). On *R. hirsutum*. AUSTRIA: Hohe Tauern, Pfandolscharte, 29 July 1891, P. Dietel (PUR F532). On *R.* ×*intermedium* Tausch. (= *R. hirsutum* × *R. ferrugineum*). AUSTRIA: Tirol, Gschnitztal (?), 2 Aug 1891, P. Dietel (PUR F533, Sydow Uredineen). On *R. kaempferi* Planch. JAPAN: Agematsu (Kiso), Shinano, 8 Aug. 1931, N. Hiratsuka (PUR F12695); Yamaguchi-mura, Chikuzen, 29 Aug. 1931, O. Ishiuchi (PUR F12696). On *R. keleticum* Balf.f & Forrest. UNITED KINGDOM: Sevenoaks, Kent, 30 Sept. 1948, W.N. Wheeler (PUR 11729). On *R. kiusianum* Makino. JAPAN: Kirishima Hotsprings, Kirishima Mts., Osumi, 25 Oct 1939, N. Hiratsuka (PUR F12694). On *R. lapponicum*. CANADA: British Columbia: Summit Pass, mi 392 Alaska Hwy., 10 Aug. 1962, W.G.Z. (DAVFP 14606). Manitoba: Ft. Churchill, 4 Sept. 1950, D.B.O.S. & W.B. Schofield (PUR 53201, ex DAOM 24977). Northwest Territories: S. Nahanni R. area, Mackenzie Mtns., 61°18′N, 124°06′W, 26 June 1970, G.W. Scotter (CAFB 3474); Indin L., Dist. Mackenzie, 64°17′N, 115°12′W, 12 Aug. 1949, W.J. Cody & B.J. McCanse (PUR 52021, ex DAOM 23509). On *R. mucronulatum* Turcz. var. *ciliatum* Nakai. KOREA: Shayu-rei, Mosan-gun, Kanhoku, 6 July 1939, N. Hiratsuka (PUR F12697). On *R. myrtifolium* Schott & Kotschy. (= *R. minus* × *R. hirsutum*). ROMANIA: Siebenbürgen, July 1883, Linhart (PUR F535). On *R. roylei*. UNITED KINGDOM: Cornwall, 27 Apr. 1954, Major Johnstone (K). On *R. suavis*. GERMANY?: May 1894, G. v. Lagerheim (PUR F534). On *R. usuriensis*. CHINA: Ji-dong-xian, Heilongjiang, L-P. Shao et al. (CFB 21586). On *R.* sp. NEW ZEALAND: Stratford, Taranaki, 14 Apr. 1924, J.C. Neill (K, Fungi of N.Z. 1714).

On *Picea abies*. ITALY: Tirol, Brixen [Bressanone], 29 July 1891, P. Dietel (PUR F527). Nr. Volga R., Piedmont, 1863, A. Carestia (PUR F513); Gressonay St. Jean, 1889, G. Briosi & F. Cavara (PUR F526). SWITZERLAND: Trail to Nair L., St. Moritz, Engadine, 18 Aug. 1998, R. Berndt (CFB 22181); Canton of Valais, 17 Aug. 1955, E. Mayor (DAVFP 11953); Gurnigel, 1883, E. Fischer (PUR F325).

C. vaccinii

On *Vaccinium parvifolium*. CANADA: British Columbia: Qualicum, Vancouver Is., 17 June 1955, W.G.Z. (PUR 54765, DAVFP 9450, Isotypes); Massett, Queen Charlotte Is., 8 Jul 1952, W.G.Z. (PUR 54528, ex DAOM 45774); nr. Empire Anchorage, Athlow Bay, Graham Is., Q.C.I., 12 June 1957, J.A. Calder & D.B.O.S. (PUR 56660, ex DAOM 59520); Long Beach, Vancouver Is., 18 May 1968, W.G.Z. (DAVFP 18160).

Peridermium zilleri

On *Picea sitchensis*. CANADA: British Columbia: Q.C.I.: Port Clements, 27 Aug. 1943, R.E. Foster (DAVFP 328, with *C. ledicola*); Alliford Bay, 12 Sept. 1988, D. Redfern (DAVFP 23794, ex DAOM 198869); Yakoun L., Graham Is., 12 Sept. 1988, D. Redfern (DAVFP 23796, ex DAOM 198870). Vancouver Is.: Port Renfrew, 15 Nov. 1972, G.W. Coombs (DAVFP 20419).

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